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Response to 13 cycles of reciprocal full-sib recurrent selection in the BS10 and BS11 maize (*Zea mays* L) populations

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**Response to 13 cycles of reciprocal full-sib recurrent selection in the BS10 and BS11
maize (*Zea mays* L.) populations.**

by

Benjamin Aaron Ford

**A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY**

Major: Plant Breeding

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has met the dissertation requirements of Iowa State University**

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INTRODUCTION

Reciprocal full-sib recurrent selection (FR) was proposed as a method of population improvement based on direct selection on the cross between prolific, synthetic maize (*Zea mays* L.) populations (Hallauer and Eberhart, 1970). Reciprocal selection methods allow breeders to exploit both general and specific combining ability in maximizing heterosis between the two populations (Comstock et al. 1949). FR relies on selection of pairs of plants based on full-sib family performance, and allows for evaluation of more individuals than does half-sib reciprocal recurrent selection (RRS). Evaluations of full-sib family performance also serve as early generation tests for S_0 individuals in each population, allowing for integration of population improvement and inbred and hybrid development objectives. As with other recurrent selection methods, objectives of FR include improvement in population means for selected characters by increasing the frequencies of favorable alleles, and the maintenance of genetic variability to allow for long-term progress.

FR was initiated in BS10 and BS11 prolific maize populations in 1963 (Hallauer, 1967a), a program currently in its 15th cycle of selection. Early evaluations of changes associated with selection have indicated improvement in grain yield, the primary trait for selection, as well as standability and maturity related traits, while maintaining genetic variability for grain yield (Eyherabide and Hallauer, 1991a; Frank and Hallauer, 1999). Simulation results suggest lower expected rates of improvement in cycles 10 through 20 of FR than in earlier cycles for most genetic models (Peiris, 2001).

The objectives of this study include the evaluation of long-term direct and indirect selection effects on the BS10/BS11 population cross and BS10 and BS11 *per se* populations, respectively, the effects of selection on heterosis and inbreeding depression in the populations and their F_1 , and the impact of FR on genetic variation and heritability in the parent populations. Response is measured for eight traits over the first 13 cycles of FR in noninbred ($F = 0$) and inbred ($F = 0.5$) BS10, BS11 and F_1 populations, with variability and heritability estimates obtained from random S_1 line evaluations. Comparisons to results in earlier cycles of selection and simulated long-term results will be used to assist in the development of models to explain observed results.

LITERATURE REVIEW

Recurrent selection is a cyclic breeding approach with two primary goals: 1) to improve the population mean for the value of some trait or traits through selection, and 2) to maintain genetic variability to allow for progress in future cycles of selection. For all methods except mass selection, the steps involved are the formation of progenies for evaluation, the evaluation of progenies, usually in replicated field trials, and the intermating of selected individuals to form the improved population. The improved population may be used as a synthetic cultivar, as a source population for the development of inbred parents and breeding lines, or as the material for initiation of another selection cycle. Methods of both inter- and intrapopulation recurrent selection have been proposed for population improvement. The comparative value of the two methods depends on the level of heterosis observed for traits of interest in the species and populations to be improved (Hallauer and Miranda-Filho, 1988).

Intrapopulation recurrent selection methods

The use of a cyclic selection procedure based on progeny evaluations for the improvement of synthetic maize (*Zea mays* L.) populations was first proposed by Jenkins (1940). Based on selection among topcrosses of random S_1 lines to the parent population, the method, referred to here as selection for general combining ability (GCA) or for additive effects (Sprague and Tatum, 1942), suggests that evaluation of lines in early stages of inbreeding is effective in the differentiation and prediction of yield potential for individual lines (Jenkins, 1935). This procedure, therefore, is more valuable for population improvement than any mass selection method. The importance and

application of improving populations, Jenkins (1940) stated, is the development of varieties for marginal maize production regions where the development and production of inbreds and hybrid varieties, as proposed by Shull (1909), “is a more hazardous and expensive undertaking”.

Based on the assumption that heterosis for grain yield is a result of overdominance, (i.e. superiority of the heterozygote over either homozygote at a large number of loci) Hull (1945) proposed a method involving a modification of Jenkins’ (1940) procedure. Whereas Jenkins (1940) suggests using the population as the tester in developing progeny for evaluation, Hull’s method involves the use of an inbred tester to select for specific combining ability (SCA) dependent primarily on non-additive effects (Sprague and Tatum, 1942). Completion of a single cycle of selection for SCA involves selection of 10 or more plants based on testcross performance, followed by recombination among selfed progeny of the selections to obtain the improved population used to initiate the next cycle (Hull, 1945). A cross of the tester line to either the improved population or inbred lines derived from it would represent the product to be utilized in commercial maize production. This proposed outcome, a hybrid variety, differs from the use of the improved population *per se* described by Jenkins (1940) for production regions where the development and use of hybrid varieties are not feasible.

Interpopulation recurrent selection methods

The lack of evidence for the relative importance of overdominance and partial dominance in the expression of heterosis led Comstock et al. (1949) to develop a selection method effective for either or both hypotheses. Referred to as recurrent

reciprocal selection (RRS), or simply reciprocal selection, the method allows for direct selection on population cross performance and greater effectiveness in improvement of traits for which both GCA and SCA are important (Comstock et al. 1949).

Using two genetically divergent populations denoted here as 'A' and 'B', the RRS method, as conceived by Comstock et al. (1949), is conducted as follows:

- 1) Year 1: 200 plants from 'A' are each crossed with four or five plants from 'B' and simultaneously selfed. In the same manner, 200 plants from 'B' are each crossed with four or five plants from 'A' and selfed. Ears resulting from the cross of an individual plant, from population A for example, with four or five others from population B, are bulked to obtain a half-sib family for testing.
- 2) Year 2: Up to 200 half-sib families from each population are evaluated in replicated tests and selections are made among families.
- 3) Year 3: Self (S_1) seed from the selections is planted and intermating within each source group is conducted to obtain the improved 'A' and 'B' populations.
- 4) Year 4: The improved populations are used to initiate the next cycle of selection.

Commercial products of RRS could involve crosses of inbred lines from the respective populations or a variety cross obtained by random mating individuals from one population to individuals from the other population (Comstock et al. 1949).

Several modifications of RRS have been proposed to simplify procedures and improve genetic gain. Russell and Eberhart (1975) suggested the use of inbred testers

derived from the reciprocal populations in forming progeny for evaluation, rather than crossing to the reciprocal populations. Their reasoning was based on the lack of evidence for a significant effect of epistasis and overdominance in heterosis.

Hand pollination can be avoided by planting intrapopulation half-sib families ear-to-row in isolation for crossing to the reciprocal population to obtain interpopulation half-sib families for testing (Paterniani and Vencovsky, 1977). Intrapopulation half-sib seed of selections is used for recombination, which results in a higher effective population size (N_e) relative to other methods under identical selection intensities (Hallauer and Miranda-Filho, 1988). A second modification requires prolificacy to allow for simultaneous outcrossing of one ear to the reciprocal population in isolation and hand pollination of the lower (second) ear using pollen bulked from desirable plants within the population (Paterniani and Vencovsky, 1978). Once again, reciprocal half-sib families are evaluated, and intrapopulation half-sib seed is recombined. Advantages to this method include a shorter cycle interval of two generations instead of three, and selection in both generations, once for combining ability and once for prolificacy. A modification of the Paterniani and Vencovsky (1977) method was later proposed for increasing expected genetic gain by allowing for selection within the intrapopulation half-sib families before recombining (Marquez-Sanchez, 1987) and therefore select directly for both *per se* performance and combining ability between populations.

Noting several disadvantages of earlier modifications, including reduced genetic gain resulting from the use of half-sib seed as the recombination unit and the complex procedures needed to form interpopulation half-sib families in the Paterniani and

Vencovsky (1977) approach, Souza Jr. (1987) suggested alternating the source of interpopulation half-sib families for testing from noninbred to inbred plants. This approach requires prolific plants from each population; the second ears of noninbred plants from a population are selfed while the upper ear is fertilized with pollen from the reciprocal population. Half-sib families harvested from the upper ears are used for testing, and the S_1 ($F = 0.5$) progenies of selected plants, based on testcross progeny performance, are used in the second “phase” of the cycle. The upper ears of S_1 progenies are fertilized with pollen from the reciprocal population to obtain reciprocal half-sib seed for evaluation while the second ears are allowed to open pollinate, resulting in recombined half-sib progenies among which selections are made based on testcross performance to begin the next cycle. The entire cycle requires two years if winter nurseries are utilized, with a higher expected genetic gain than RRS or any previously proposed modifications (Souza Jr., 1987).

A modification of recurrent reciprocal selection (Comstock et al. 1949) using full-sib rather than half-sib progenies was introduced by Hallauer and Eberhart (1970). Referred to here as full-sib reciprocal recurrent selection (FR), the procedure involves pairs of S_0 plants from reciprocal populations which are simultaneously crossed and selfed to obtain interpopulation full-sib families for testing, and selfed seed for recombination of selected entries and inbred line development. In the original scheme, prolific populations are required to allow for production of full-sib and selfed seed on the same plant (Hallauer and Eberhart, 1970). Pollinations are made by first crossing pairs of plants from opposite populations using the second ears, followed by self pollination of

the top ears one or two days later to ensure seed development on the second ear (Hallauer, 1967a; Lonnquist and Williams, 1967).

The use of non-prolific material is possible if reciprocal crosses between S_1 progeny of a pair of S_0 plants from opposite populations are made, but the number of generations required to complete a cycle of selection increases (Hallauer, 1967b). Hallauer (1973) described a procedure in detail for FR in non-prolific material. Two other modifications of the original FR procedure for use in one-eared populations involve full-sib or “self-sib” mating for producing seed for recombination (Marquez-Sanchez, 1982) in order to reduce the amount of inbreeding relative to self pollination.

Selection among full-sib families may be based entirely on grain yield, or a selection index may be developed and employed to consider agronomic traits such as stalk breakage and disease resistance as well (Hallauer and Eberhart, 1970). Selection on multiple traits requires a sacrifice in the expected rate of gain for yield, but other traits are critical in the development and commercial production of maize populations, inbreds, and hybrids. Following evaluation of pairs of plants based on full-sib family performance, selfed seed from S_0 parents of a selected $S_0 \times S_0$ cross is used for recombination to form the two improved populations from which the next cycle of selection will be initiated.

The use of selfed progeny of selected $S_0 \times S_0$ crosses for recombination provides the opportunity for inbred and hybrid development in addition to population improvement. The initial evaluation of full-sib progenies serves as an early generation test for combining ability (Hallauer and Eberhart, 1970), allowing selfed (S_1) seed of parents of desirable crosses to be planted in the breeding nursery and reciprocally crossed

and evaluated during further generations of inbreeding as described by Hallauer (1967a) and Lonnquist and Williams (1967).

Theoretical effects of interpopulation selection

Mean and variance

The magnitude and rate of response to reciprocal recurrent selection are dependent on genotypic variances in the base populations and population cross and, therefore, on initial allele frequencies. To examine the effects of these factors on predicted progress, it is necessary to understand mean and variance models on the basis of allele frequencies.

The contribution of a single locus to the genotypic or phenotypic mean of a population is given by the equation:

$$M = a(p-q) + 2dpq,$$

where p is the frequency of the favorable allele, q is the frequency of the non-favorable allele, a is the value of the homozygote, and d is the value of the heterozygote (Falconer and Mackay, 1996). The mean summed over all loci is maximized when all loci are fixed for the favorable allele ($p = 1$), assuming no overdominance.

Total genetic variance (σ^2_G) for a given locus represents a sum of both additive and non-additive genetic variances, and is given by the equation:

$$\sigma^2_G = \sigma^2_A + \sigma^2_D = 2pq[a+d(q-p)]^2 + (2pqd)^2,$$

where σ^2_A is the additive variance and σ^2_D is the dominance variance (Falconer and Mackay, 1996). It is important to note that additive variance does not imply additive gene action, and only the absence of any contribution of dominance variance to total

genetic variance allows the conclusion that dominance and epistasis are not significant for a given character. If total genetic variance is entirely additive ($d = 0$), σ^2_G is maximized when $p = q = 0.5$, whereas under complete dominance ($a = d$), σ^2_A is maximum when q (the recessive allele) = 0.75, σ^2_D is maximum at $p = q = 0.5$ and σ^2_G is maximum at $q = 0.71$. True overdominance results in two maxima for σ^2_A , one at $q = 0.15$ and the other at $q = 0.85$, and a maximum for σ^2_D at $p = q = 0.5$. Therefore, loci with intermediate allele frequencies make the largest contributions to genetic variance (Falconer and Mackay, 1996).

The expected results of interpopulation recurrent selection at a single locus (represented as the B locus) under varying levels of dominance are defined by Comstock (1996). For interpopulation methods, direct effects of selection are on the population cross, with indirect effects on the populations *per se*. In the case of partial dominance, selection is expected to fix the favorable allele ($p = 1$) in each of the base populations, resulting in a genotype of BB for the population cross. Under complete dominance, the favorable allele would be fixed in one of the two populations, with the final outcome in the reciprocal population determined by factors other than selection. The resulting genotype for the population cross would be BB or Bb. Overdominance would result in selection for the heterozygote (Bb) in the population cross, requiring the fixation of one of the two base populations for the favorable allele, and the other for the non-favorable allele. Assuming selection is the only factor affecting allele frequency, reciprocal recurrent selection (full-sib or half-sib) will always result in the most favorable genotype at each locus under any level of dominance (Comstock, 1996). Selection, however, is not

the only factor in determining final allele frequencies. Within the constraints of a finite effective population size (N_e), recurrent selection likely will not result in the fixation of the favorable allele (i.e., $p = 1$) for all loci, as fixation for any allele at any locus may occur by random chance (Comstock, 1996), a phenomenon known as drift. The expected change in the population mean due to drift is zero (Robertson, 1960), although fixation as a result of drift will serve to reduce genetic variability.

Genetic gain

Expected genetic gain from interpopulation recurrent selection is determined from additive and dominance variances estimated for the population cross, rather than the individual base populations, as the population cross is the direct subject of selection. The expected response calculated also refers only the population cross and does not apply to the base populations *per se*. Expected genetic gain per cycle (G_C) equations for RRS and FR as presented by Sprague and Eberhart (1977) are as follows:

RRS:

$$G_C = \frac{k \frac{1}{4} \sigma^2_{A(1)}}{\sqrt{(\sigma^2_{E(1)}/rm) + (\frac{1}{4} \sigma^2_{AE(1)}/m) + \frac{1}{4} \sigma^2_{A(1)}}} + \frac{k \frac{1}{4} \sigma^2_{A(2)}}{\sqrt{(\sigma^2_{E(2)}/rm) + (\frac{1}{4} \sigma^2_{AE(2)}/m) + \frac{1}{4} \sigma^2_{A(2)}}},$$

where numbers in parenthesis refer to populations 1 and 2, and

FR:

$$G_C = \frac{k \frac{1}{2} \sigma^2_A}{\sqrt{(\sigma^2_E/rm) + [(\frac{1}{2} \sigma^2_{AE} + \frac{1}{4} \sigma^2_{DE})/m] + \frac{1}{2} \sigma^2_A + \frac{1}{4} \sigma^2_D}}.$$

Variables in the two equations include σ^2_E , the experimental variance, σ^2_A , the additive variance, σ^2_D the dominance variance, σ^2_{AE} , the additive by environment interaction

variance, σ^2_{DE} , the dominance by environment interaction variance, k , a standardized selection differential for normal distributions and function of the intensity of selection, r , the number of replications per environment, and m , the number of environments utilized in evaluation of progenies formed for selection (Sprague and Eberhart, 1977). Values for k can be calculated using the derivation described by Falconer and Mackay (1996). Values of k for commonly used selection intensities include 2.06 (5 percent selection intensity), 1.75 (10 percent), 1.55 (15 percent), and 1.40 (20 percent). The fraction coefficients for the variance terms in the equations for RRS and FR are derived from the covariance of relatives for half-sib and full-sib families, respectively (Sprague and Eberhart, 1977).

Genetic gain calculations indicate improved selection response per cycle with higher selection intensities. While effective for short-term selection response, higher selection intensities without increases in the number of progenies tested reduce the number of selected families and increase the frequency of random drift (Robertson, 1960; Rawlings, 1970). The loss of genetic variability as a result of drift limits gain in future selection cycles. An optimal selection intensity for both long-term and short-term progress must be high enough to achieve sufficient gains, but low enough to limit drift resulting from low effective population size. Based on considerations of a number of initial allele frequencies and probabilities of fixation due to selection or drift, the use of a selection intensity near 10 percent and effective population size of 20 to 30 selected families is appropriate (Rawlings, 1970).

The dependence of genetic variance and its components on allele frequencies indicates that changes in frequencies due to selection or drift, which accumulate over cycles of selection, will lead to changes in variance, and, therefore, changes in expected gain per cycle (Falconer and Mackay, 1996). While a linear selection response is generally assumed during early cycles, these changes in variance over many cycles would theoretically result in a non-linear response per cycle (Eberhart, 1964). Initial favorable allele (p) frequencies near or above 0.5 would lead to a quadratic response, as variance over cycles would decrease due to increases in frequency or fixation of favorable alleles through selection. This expectation is expressed as:

$$Y_i = \mu_0 + \beta_1 X_i + \beta_2 X_i^2 + \delta_i ,$$

where the response (Y_i) is a sum of the mean (μ_0), the deviation from regression (δ_i) and the linear and quadratic regression terms ($\beta_1 X_i$ and $\beta_2 X_i^2$) (Eberhart, 1964). Addition of a cubic term to the model is appropriate when low desirable allele frequencies in the base populations result in an initial increase in genetic variance before decreasing in later cycles (Eberhart, 1964).

The calculation of expected selection response for a single trait carries with it an assumption of true and accurate truncation selection for the character or trait considered (Falconer and Mackay, 1996). In cases where index selection is used to simultaneously select for several traits, the assumption is violated, and improvement in any one of the traits will be less than would be expected or possible with consideration of only a single trait (Hallauer, 1967a). The importance of many traits other than yield, however, has led

to the use of selection indices in some form for nearly all reciprocal recurrent selection applications.

Heterosis

Heterosis can be described as the superiority of a hybrid or population cross relative to either the mid-parent value or the value of the highest performing parent. Loci for which the level of dominance (d) is not equal to zero contribute to the level of heterosis, here expressed as the mean of the population cross (M_{F_1}) relative to the mid-parent value (MP). If y is defined as the difference in allele frequencies between two random mating base populations ($y = p - p' = q' - q$, where p and q are the frequencies of two alleles in the first population and p' and q' are the frequencies of the same alleles in the second population), then the means of the mid-parent and population cross as described by Falconer and Mackay (1996) are as follows:

$$MP = a(p - q - y) + d[2pq + y(p - q) - y^2], \text{ and}$$

$$M_{F_1} = a(p - q - y) + d[2pq + y(p - q)].$$

Mid-parent heterosis for a single locus, therefore, can be expressed as:

$$H_{MP} = M_{F_1} - MP = dy^2.$$

Summed over all loci, heterosis is observed when dominance at multiple loci is directional, as the effects of loci dominant in opposite directions may cancel each other (Falconer and Mackay, 1996). Expressed as a percentage, mid-parent heterosis (H_{MP}) for a given trait is calculated as:

$$H_{MP}(\%) = \frac{M_{F_1} - MP}{MP} \times 100.$$

High-parent heterosis (H_{HP}) is calculated by substitution of the value for the best performing parent for the mid-parent mean in the above equation.

Inbreeding depression

Inbreeding depression in the context of reciprocal recurrent selection is measured as the performance the population cross or either of the *per se* populations relative to their corresponding inbred populations. If the inbreeding coefficient (F) is defined as zero for the *per se* populations or the population cross, selfing of random plants in one of these populations would produce a progeny population with an F value of 0.5. The expected mean value of the inbred population (M_F) relative to the noninbred population mean (M_0) for a given locus expressing dominance is defined by Falconer and Mackay (1996) as:

$$M_F = M_0 - 2dpqF.$$

It is important to note that fixation of the favorable allele by selection, or of either allele by random drift in the population cross or one of the *per se* populations, results in elimination of an inbreeding depression effect for that locus on the mean of the corresponding inbred population. The effect of inbreeding depression on the inbred population mean is maximum at $p = q = 0.5$ (Falconer and Mackay, 1996).

Simulated progress from FR and RRS

Computer simulations of recurrent selection progress require simplified genetic situations. General conclusions, therefore, are only possible through inference from the specific conditions defined (Cress, 1967). The length of time and number of resources necessary for application and field evaluation of reciprocal recurrent selection methods,

however, make simulations attractive for comparisons and predicted response. Several simulations of RRS and FR have been reported (Cress, 1967; Ehdaie and Cress, 1973; Jones et al. 1971; Martin and Hallauer, 1980; Peiris, 2001).

Cress (1967) evaluated the simulated results of RRS and two proposed modifications of the procedure using the Monte Carlo method. The models considered 40 independent loci additively affecting a quantitative character with low heritability. A diploid organism with two alleles per locus was assumed, on which 20 cycles of selection were simulated using two populations of 90 individuals per generation. From these individuals, the 10 best progenies were selected each cycle. Three non-identical sets of initial frequencies of favorable alleles were considered for complete dominance and purely overdominance models.

RRS in these simulations was effective for improvement of the hybrid, or population cross, for dominance and overdominance models for all initial conditions (Cress, 1967). Progress in hybrid performance was approximately linear over the 20 cycles of selection for the complete dominance model when initial frequencies were equal to 0.1 for populations A and B (i.e. $p_A = 0.1$, $p_B = 0.1$). However, progress tapered off slightly when p_A began at intermediate or high frequencies. Hybrid improvement under overdominance was approximately linear under all defined conditions.

Changes in performance of the populations *per se*, the indirect units of selection, were substantially different for the two models (Cress, 1967). Greater selection pressure was evident on the population with higher initial favorable allele frequencies, but in general, RRS was not effective for significantly improving *per se* performance of the

base populations. *Per se* performance actually decreased over long-term selection when overdominance was considered. However, improvement over the first few cycles may be observed in overdominance models under certain initial allele frequency conditions, preventing the presentation of improved short-term *per se* performance resulting from RRS as evidence against the role of overdominance in heterosis (Cress, 1967).

Martin and Hallauer (1980) also reported simulation results for RRS using 40 independent loci with two alleles per locus. Initial allele frequencies were defined as $p_A = p_B = 0.5$ and $p_A = 0.5, p_B = 0.25$ for complete, partial, and no dominance models. Hybrid performance exceeded improvement in population *per se* performance in all simulations. On the basis of correlations between simulated progress and observed response to seven cycles of RRS in BSSS and BSCB1 maize populations, actual progress most closely matched a completely dominant model with initial allele frequencies of $p_A = p_B = 0.5$ (Martin and Hallauer, 1980).

A comparison of FR and RRS was conducted using algebraic comparisons and computer simulation that evaluated predicted response over 20 cycles of selection (Jones et al. 1971). Algebraic calculations using a defined set of variances indicated that the selection differential for FR would need to be 1.2 times larger than that for RRS to achieve similar rates of progress. This is feasible, however, as more families can be evaluated for FR than for RRS with similar testing resources.

Under simulation models considering 28 loci with two alleles per locus, the rates of progress over the final 10 cycles of selection were generally lower than for the first 10 cycles, in part due to the small effective population sizes modeled (Jones et al. 1971).

Models considered were additive, complete dominance, and multiplicative and complementary epistasis with 10 individuals selected from 20 and 40 families evaluated for RRS and FR, respectively. While the population sizes and selection intensities utilized in this simulation were unrealistic (Peiris, 2001), FR generally resulted in greater progress than RRS for the defined conditions. Advantages of FR over RRS were most evident with lower selection intensities and higher environmental, relative to genetic, variances (Jones et al. 1971).

Peiris (2001) utilized a more realistic set of initial conditions and selection procedures in simulating response to FR and RRS under 22 different genetic situations. A 10 percent selection intensity exerted on a constant population size of 110 diploid individuals each cycle was followed through 20 cycles of selection. Two sets of initial allele frequencies, $p_A = p_B = 0.5$ and $p_A = 0.75, p_B = 0.25$ were combined with 11 different genetic models including additive gene action, partial dominance, complete dominance, overdominance, and seven models involving epistasis. Also evaluated were effects of changes in defined conditions, including linkage, selection intensity (increased to 20 and 30 percent), number of loci involved (altered from 40 to 20 and 80) and the effect of environment on the character simulated.

Results suggested no significant advantage of either RRS or of FR for 21 of 22 sets of conditions modeled (Peiris, 2001). Only for dominance-by-dominance epistasis and equal allele frequencies with S_1 plants as recombination units did RRS hold a significant advantage, although RRS regression coefficients were slightly greater for most genetic situations. Linear and quadratic coefficients for cycles were significant

(probability of a greater $F < 0.01$) for all models with the exception of RRS under additive-by-additive epistasis, unequal allele frequencies, and S_1 recombination units.

Simulated response in the hybrid populations was generally greater than that in the *per se* populations (Peiris, 2001). Partial dominance with equal initial allele frequencies, complete dominance, overdominance, and epistasis all showed greatest response in the hybrids, while the parent population with the higher initial allele frequency ($p = 0.75$) showed a greater simulated improvement under partial dominance. In nearly all cases, the rate of response in the hybrid decreased in later cycles of selection (Peiris, 2001).

Empirical evaluations of response to RRS

Early evaluations of progress

Reports in a number of maize populations indicate successful application of RRS in a diverse group of genetic backgrounds. Grain yield has consistently been the exclusive or primary trait emphasized in selection, although selection indices have been utilized in some cases to include consideration of grain moisture, root lodging, stalk breakage, or other traits. While not compared for all selection programs, the direct response to selection in the population cross has generally exceeded the indirect response in the parent populations *per se*. Gevers (1975), however, reported an improvement in grain yield of 7.9 percent per cycle in Teko Yellow and 6.0 percent in Natal Yellow Horsetooth compared with a 6.0 percent increase per cycle in the F_1 cross over three cycles of RRS.

Moll and Hanson (1984) found a 2.7 percent gain per cycle in the F_1 cross of Jarvis and Indian Chief, which showed *per se* improvement at rates of 2.4 percent and -0.3 percent, respectively. These gains were realized over 10 cycles of RRS, although a lack of significant change in performance of either population or the F_1 was noted over the final two cycles. This “plateau” may be temporary and possibly associated with a lack of further improvement in prolificacy, which had improved along with grain yield over the first eight cycles (Moll and Hanson, 1984). An increase in mid-parent heterosis from 29.4 percent in the cycle 0 population cross to 40.7 percent in the cycle eight F_1 population was observed as well (Moll and Hanson, 1984).

Results from modified RRS

Modified RRS procedures have been proposed and successfully implemented in Tuxpeño and flint populations (Paterniani and Vencovsky, 1977; Paterniani and Vencovsky, 1978). One cycle of modified RRS in Piramex, a yellow dent Tuxpeño population, and Cateto, an orange flint resulted in *per se* improvements of 6.9 and 4.8 percent and a 7.5 percent increase in the population cross (Paterniani and Vencovsky, 1977). The second proposed modification of RRS was accompanied by a reported 3.5 percent per cycle increase in F_1 population performance after three selection cycles (Paterniani and Vencovsky, 1978). Progress was not assessed in either the Dent Composite (Tuxpeño) or the Flint Composite parent populations.

Menz-Rademacher et al. (1999) compared results from RRS and an RRS modification using an inbred tester (Russell and Eberhart, 1975) in BS21 and BS22. After six cycles of selection, RRS increased population cross performance by 4.4 percent

per cycle compared with a 1.6 percent per cycle for modified RRS. Improvement in high-parent heterosis in the F_1 , initially at 1.0 percent in the cross of the cycle 0 populations, was also greater for RRS (up to 25.4 percent) than for modified RRS (up to 17.2 percent) after six selection cycles (Menz-Rademacher et al. 1999).

RRS in BSSS and BSCB1

An RRS program was initiated in 1949 in Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic No. 1 (BSCB1) and is still underway. Selection has been conducted primarily for grain yield, although grain moisture, stalk lodging, and root lodging have also been considered. A selection index using heritabilities as weights, as suggested by Smith et al. (1981), was employed beginning with cycle nine for all four traits. Several evaluations of selection progress have been reported, including Penny and Eberhart (1971), Eberhart et al. (1973), Martin and Hallauer (1980), Smith (1983), Helms et al. (1989a and 1989b), Keeratinijakal and Lamkey (1993a and 1993b) and Schnicker and Lamkey (1993).

A recent evaluation by Keeratinijakal and Lamkey (1993a) indicates a 6.95 percent per cycle direct response to 11 cycles of RRS for grain yield, while indirect response measured 1.66 percent per cycle in BSSS and 1.94 percent in BSCB1. Schnicker and Lamkey (1993) reported a 6.46 percent per cycle increase in population cross performance over the same period. Keeratinijakal and Lamkey (1993a) cited the use of lower selection intensities (intermating 20 rather than 10 S_1 progenies to form improved populations) after cycle eight and a switch from RRS to FR after cycle nine as possible reasons for a lack of observed progress in cycles 10 and 11 for grain yield either

in the population cross or the parent populations. Changes in other selected traits included decreases in root lodging and stalk lodging percentages for the population cross, although grain moisture increased slightly (Keeratinijakal and Lamkey, 1993a; Schnicker and Lamkey, 1993). Also noted was an increase in mid-parent heterosis for grain yield, from 25.4 percent in $C_0 \times C_0$ to 76.0 percent in $C_{11} \times C_{11}$ (Keeratinijakal and Lamkey, 1993a).

Smith (1979) proposed a generation means analysis model to evaluate changes in allelic frequencies based on observed changes in population means following recurrent selection. Use of the Smith model for evaluating progress indicates a greater role of dominance effects and little effect of overdominance in the observed increase in grain yield performance for BSSS \times BSCB1 (Keeratinijakal and Lamkey, 1993b). Dominance effects were of primary importance for improved *per se* performance in BSCB1, but increases in BSSS performance were attributed to both additive and dominance effects. Significant genetic drift effects on increases in *per se* performance have been noted for the first 10 cycles of RRS in BSSS (Helms et al. 1989a) and for both parent populations over eight cycles (Smith, 1983).

Calculations of changes in genetic variance components differ among studies. An increase in σ^2_A for grain yield, plant height, and ear height, and decreases in σ^2_A for root lodging and stalk lodging and in σ^2_D for all traits except grain yield accompanied a 6.06 percent per cycle observed increase in interpopulation grain yield performance over nine cycles of RRS (Betran and Hallauer, 1996a and 1996b). Schnicker and Lamkey (1993) observed a non-significant decrease in σ^2_G for yield and significant decreases in

variability for root lodging, stalk lodging, and anthesis and silking dates. While these reports suggest RRS has been successful in increasing mean performance without significant losses in variability, Helms et al. (1989b) and Holthaus and Lamkey (1995a and 1995b) indicated either significant or nearly significant decreases in variance components for grain yield in BSSS over 9 and 11 cycles of RRS, respectively. Additive variance in BSSS accounted for the majority of σ^2_G for all traits with the exception of grain yield (Holthaus and Lamkey, 1995b).

Inbreeding depression (ID), measured as a percentage decrease in mean from a non-inbred (S_0) population to its inbred (S_7) counterpart, decreased as a result of selection for most traits in BSSS and BSCB1 over nine cycles of selection (Benson and Hallauer, 1994). Decreases in ID for the selected traits grain yield, root lodging, and stalk lodging, and for non-selected traits, including plant height and ear height, were observed for both populations, with the exception of root lodging in BSCB1. This, the authors assert, “suggests that [the improved] populations were segregating at fewer loci or selection had increased the allele frequencies beyond 0.5” (Benson and Hallauer, 1994). Inbreeding depression in BSSS x BSCB1, measured by selfing the population cross, increased over 11 cycles suggesting selection for complementary alleles in the two populations and a subsequent increase in heterozygosity in the F_1 (Keeratinijakal and Lamkey, 1993a).

Molecular genetic approaches provide avenues for direct assessment of changes in allele frequencies. Labate et al. (1999) used 82 restriction fragment length polymorphism (RFLP) loci to examine changes in allele frequency as a result of RRS in BSSS and BSCB1 through 12 cycles of selection. Of the alleles present in progenitor populations,

approximately 30 percent were extinct or nearly extinct (allele frequencies of 0.10 or less) and 10 percent of loci were near fixation (frequencies from 0.90 to 1.0) in cycle 12 populations. Loci nearing fixation were not the same for BSSS and BSCB1, suggesting selection for complementary alleles at loci in each of the populations. While the relative effects of random genetic drift and selection on changes in allele frequencies cannot be assessed directly, differences between cycle 0 and cycle 12 populations were not entirely due to drift. Evidence for this included the 17 percent of loci for which the null hypothesis that genetic drift could have accounted for observed changes was rejected (Labate et al. 1999).

FR in BS10 and BS11

Effects on means

The prolific Iowa Two-ear Synthetic (BS10) and Pioneer Two-ear Synthetic (BS11) were used to initiate a FR program in 1963 (Hallauer, 1967a). Selection, now in the 15th cycle, has focused primarily on grain yield, with consideration given to root and stalk lodging and grain moisture. Prolificacy, a trait with complex and genotype dependent inheritance (Hallauer, 1974), is selected for during formation of full-sib families and may contribute to improvement in and stable expression of grain yield (Collins et al. 1965; Hallauer, 1973). Evaluations of direct and indirect response to early cycles of selection have been reported (Obilana et al. 1979; Hallauer, 1984; Eyherabide and Hallauer, 1991a).

Hallauer (1984) reported a 2.1 percent per cycle increase in grain yield through cycle six for the population cross, with indirect responses of 2.7 percent per cycle in

BS10 and 2.4 percent per cycle in BS11. Most improvement in the yield of BS11 was made in the first cycle of selection. An improvement in stalk lodging was noted, but little change was evident in root lodging, dropped ears, and grain moisture. Obilana et al. (1979) observed a 6.3 percent per cycle response (direct) to selection and responses (indirect) of 5.5 percent in BS10 and 6.0 percent in BS11; they suggested that improvement over earlier cycles of selection could largely be explained by improvements in the base populations.

Eyherabide and Hallauer (1991a) evaluated alternate cycles of selection from C0 to C8 for the interpopulation cross, BS10 and BS11 at non-inbred ($F = 0$) and inbred ($F = 0.5$) stages. Linear response in grain yield was 6.5 percent per cycle for the population cross and 1.6 percent per cycle for BS11. A quadratic response was observed for BS10, and improvement from C0 to C8 was calculated at 3.0 percent per cycle. Improvements in the corresponding inbred populations were 5.4, 5.8, and 6.9 percent in BS10, BS11, and the population cross, respectively. Improvements were also significant for stalk lodging and prolificacy in the population cross and both parent populations, root lodging in BS11, and grain moisture and ear height in the population cross and BS11.

Values for parameters in the Smith model were estimated to provide genetic interpretation of changes observed through cycle eight (Eyherabide and Hallauer, 1991b). Estimates suggest improvement in grain yield by selection for loci with additive effects in BS11 and dominance effects in BS10. Increases in mean grain yield for the base populations have been limited by genetic drift. Reduced stalk lodging in BS10 primarily

involved alleles with additive effects, while dominance effects were important for root and stalk lodging improvement in BS11.

Changes in inbreeding depression and heterosis were observed in selected populations (Eyherabide and Hallauer, 1991a and 1991b). Percentage inbreeding depression from non-inbred to corresponding inbred populations decreased from 56.1 to 37.9 percent in BS11 and from 42.4 to 32.9 percent in BS10 from C0 to C8. These changes were attributed to an increase in homozygotes for favorable alleles in the populations *per se*. The rate of inbreeding depression increased slightly in the population cross, likely due to an increase in the frequency of heterozygotes. Mid-parent heterosis for grain yield measured in the population cross increased from 2.5 percent in C0 x C0 to 39.7 percent in C8 x C8, while High-parent heterosis increased from -5.5 to 34.2 percent. The changes in heterosis “suggest that FR either caused changes in the frequency of genes with dominant effects in a different set of loci for each population or selected different isoalleles with dominant effects in each population” (Eyherabide and Hallauer, 1991a).

Effects on variances

The importance of maintaining genetic variability to allow for continued response to selection led to periodic evaluations of variability in BS10 and BS11 (Lantin and Hallauer, 1981; Hallauer, 1984; Reeder et al. 1987; Frank and Hallauer, 1999). Early studies based on evaluations of interpopulation genetic variance found no evidence for decreased variance after four (Lantin and Hallauer, 1981) and seven (Hallauer, 1984) cycles of FR for grain yield. Selection, therefore, should be effective in later cycles.

Reeder et al. (1987) used 50 full-sib and 100 S_1 families each from BS10C0, BS10(FR)C6, BS11C0, and BS11(FR)C6 to estimate intrapopulation genetic variance components. Non-significant decreases in additive genetic variance were noted for grain yield, stalk lodging, and ear height in both base populations, while dominance variance estimates were slightly higher in C6 than C0 populations for stalk lodging and ear height and for grain yield in BS10. Complementary changes occurred in nearly all cases in additive by environment and dominance by environment interaction variances.

Frank and Hallauer (1999) formed full-sib families for C0 and C10 populations to estimate changes in inter- and intrapopulation variances. Significant decreases in σ^2_G in the interpopulation cross were detected for stalk lodging, root lodging, and dropped ears, while grain yield σ^2_G increased slightly. Only the estimate for stalk lodging decreased in BS10, while significant decreases for BS11 included estimates for grain moisture, root and stalk lodging, dropped ears and days to mid-silk and mid-anthesis. A nonsignificant decrease for grain yield genetic variance was measured for BS10. While general downward trends were calculated for plant and ear height score variances, and for variances for all other agronomic traits, the maintained genetic variance for grain yield suggests selection will be effective in cycles beyond C10.

Inbred line extraction from FR

Aside from their effectiveness in identifying at S_0 the best families for intermating (Rodriguez and Hallauer, 1991), FR procedures also provide an early test for inbred line development (Hallauer, 1973). S_1 seed used for recombination of selected full-sib family entries can then be sampled to allow for continued inbreeding and testing to produce

superior inbreds and hybrids. Based on evaluations of inter- and intrapopulation crosses from $S_0 \times S_0$ to $S_4 \times S_4$, Hoegemeyer and Hallauer (1976) determined that FR was successful in identifying lines with high SCA with its tester from the reciprocal population and high GCA in crosses with other elite lines. Superior inbred lines released from Iowa State University derived from the FR program include B79 from BS10C0 (Russell and Hallauer, 1976), B77 from BS11C0 (Russell and Hallauer, 1975), B98 from BS11(FR)C5 (Hallauer et al. 1994) and B113 (Hallauer et al. 2000) and B115 (Hallauer et al. 2001) from BS11(FR)C9.

MATERIALS AND METHODS

Populations and selection procedures

FR was first implemented in Pioneer Two-ear Composite (PHPRC), developed by W.L. Brown at Pioneer Hi-Bred International, and Iowa Two-ear Synthetic (BSTE), developed at Iowa State University by W.A. Russell, because of the prolific nature of the two populations (Hallauer, 1967a; Hallauer, 1973). The first full-sib families between PHPRC and BSTE, later designated BS11 and BS10, respectively, were produced in 1963 (Hallauer, 1967a). The FR program in BS10 and BS11 is currently in its 15th cycle.

Self and full-sib seed were produced on prolific pairs of plants from opposite populations in the first selection cycle by selfing the second ears and crossing to the top ears on the same day (Hallauer, 1973). Difficulty in obtaining enough seed for evaluation and recombination led to the practice in later cycles of crossing to the second ears to produce full-sib seed one day before selfing the top ears of a pair of S_0 plants. Selected S_5 lines from the original populations were intermated to form the cycle one populations, with S_1 seed used for recombination in subsequent cycles (Hallauer, 1973).

Selection for stalk quality in early cycles was practiced on S_0 plant pairs, with selected full-sib families advanced to replicated evaluations (Hallauer, 1984). Field evaluations have focused primarily on grain yield, with consideration given to grain moisture, stalk lodging, and root lodging. Selections after cycle six have included these four traits in a selection index, weighted by their heritabilities as suggested by Smith et al. (1981). Twenty-four S_5 lines from BS10 and 18 from BS11 were used for

recombination to form the respective cycle one populations. S_1 seed intermated in subsequent cycles corresponds to 20 selected full-sib families in each cycle from replicated trials. The number of full-sib families tested during the first seven FR cycles ranged from 144 to 247 (Hallauer, 1984).

Genetic materials for this study

Accurate evaluations of progress from FR and comparisons among populations require seed for included entries to be of similar quality. Seed for 64 entries was produced in the breeding nursery in Ames in 1999 and in the 1999-2000 Puerto Rico winter nursery. Inbred, noninbred, and interpopulation cross seed were produced from non-inbred BS10 and BS11 populations representing cycles 0, 1, 3, 5, 7, 9, 11, and 13 of selection. Assortative matings and reciprocal crosses between pairs of plants were avoided in intermating and crossing. Inbred seed of the interpopulation crosses was obtained by selfing the non-inbred interpopulation cross entries in the winter nursery.

Approximately 100 ears produced for each population were equally sampled to form bulks. Duplicate bulks for cycle 0 and cycle 13 entries were independently sampled to allow for the planting of duplicate entries of these populations in field trials, allowing for improved estimates of endpoint means and lower standard errors for regression coefficients. Population entries in field evaluations, therefore, included two entries each for BS10 noninbred, BS10 inbred, BS11 noninbred, BS11 inbred, interpopulation cross noninbred, and interpopulation cross inbred for cycle 0 and cycle 13 populations, with single entries for their respective cycle 1, 3, 5, 7, 9 and 11 populations. B77/B73,

B79/Mo17, B73/Mo17, and the F_2 population of B73/Mo17 were included as hybrid checks, making a total of 64 entries used in evaluating changes associated with FR.

A second experiment utilized remnant seed following the sampling of S_1 ears to form bulks used in the first experiment. Sixty-five S_1 lines from BS10C0, BS10C13, and BS11C13, and 42 lines from BS11C0, were evaluated to estimate the effects of FR on intrapopulation genetic variance. Seed set on hand-pollinated ears was the limiting factor on the number of lines included in the evaluation.

Field evaluation procedures

Sixty-four entries for evaluating changes associated with 13 cycles of FR were randomized in an 8 x 8 simple lattice design and planted in 2000 at a diverse set of one Nebraska and nine Iowa locations between April 21 and 29. Iowa State University (ISU) locations included Ames, Ankeny, Lewis, Rippey, Carroll, Fairfield, and Crawfordsville, Iowa. The Clarence and Grinnell, Iowa locations were operated by Cargill Seeds Inc., while the J.C. Robinson Seed Co. (Golden Harvest) managed the Fremont, Nebraska location. This experiment was designated as experiment one.

All plots consisted of two rows spaced 0.762 meters, with plot lengths of 5.486 meters for ISU locations, 5.334 meters for Cargill locations, and 7.163 meters at Fremont, Nebraska. Plots were overplanted and thinned at the five-leaf stage to uniform stands of 67,737 plants ha^{-1} , 68,835 plants ha^{-1} , and 66,923 plants ha^{-1} at Cargill, J.C. Robinson, and four ISU locations, respectively. Plots at Rippey, Carroll and Fairfield were planted at 74,094 plants ha^{-1} and were not thinned.

The 237 entries for examining changes in intrapopulation genetic variability were evaluated in 2000 in a split-plot design blocked by replications and populations to limit the effects of neighboring plot plant heights on variance estimates and entry means. Two replications were planted at Ames on April 21 and at Ankeny on April 27, with plot dimensions identical to previously described in experiment one for these locations. Plots were overplanted and thinned to uniform stands of 59, 753 plants ha⁻¹ at the five-leaf stage. As with experiment one, all plots for this experiment were machine planted. This experiment will be referred to herein as experiment two.

Traits measured for experiment one include grain yield measured in quintals per hectare (q ha⁻¹) and adjusted to a 15.5 percent grain moisture basis, grain moisture (expressed as a percentage), root and stalk lodging (as a percentage of counted stands), plant and ear heights (as an average in centimeters of measurements from 10 random plants per plot), and days to mid-anthesis and mid-silk (calculated as the number of days from planting to 50 percent anther and silk extrusion, respectively). A late season hail storm at Lewis and immeasurably low grain yields for most entries at Clarence and Grinnell made trait measurements at these locations impossible. These three locations were not included in analyses. Grain yield and moisture were measured at the remaining seven locations, with root and stalk lodging measured at Ames, Ankeny, Carroll, Rippey, Fairfield, and Fremont, plant and ear heights at Ames, Ankeny, Carroll, and Rippey, and days to mid-anthesis and mid-silk at Ames and Ankeny. All traits listed were measured for experiment two at both Ames and Ankeny. All plots for both experiments were machine harvested between September 20 and October 4.

Statistical methods

Experiment one

Analyses of variance appropriate for a randomized complete block design with environments and replications as random effects and entries as fixed effects were performed for each of eight traits, with partitioning of entry and entry by environment interaction sums of squares into within populations, within duplicate entries, and among populations. Within population sums of squares were further partitioned into linear, quadratic, and deviations sums of squares. Total and pooled error degrees of freedom for grain yield and grain moisture were adjusted for missing values, for which the plot measurements for the other replication were imputed. Total missing values for grain yield were five out of a total 896 plots, and 10 missing values of 896 for grain moisture. Bartlett's test for homogeneity was used for testing the assumption of homogeneous error variances. Cycle one entries were excluded from all analyses, due to observations and results suggesting the possibility of a contaminated seed source.

Tests for significance make use of the F-statistic and were displayed as significant at probabilities of greater F values ($\text{probF} < 0.05$) or highly significant at $\text{probF} < 0.01$. The main effects of environments were tested with the replications within environment mean squares. Significances of main effect and partitioned mean squares for entries were tested with the corresponding environment interaction mean squares, while entry by environment main effect and partitioned mean squares were tested with the pooled error term.

Regression analyses were performed fitting linear and quadratic models, as suggested by Eberhart (1964) for evaluating long-term selection response, as determined by significance of linear and quadratic mean squares. Standard errors of intercepts and linear and quadratic regression coefficients were calculated along with R^2 values, used to indicate the proportion of the total variation explained by the model presented. Linear trends were graphically evaluated for all traits, regardless of linear fit to the data.

Standard errors of means calculated separately for C0 and C13 means, for which there were two times the number of replications, and for either non C0 or non C13 means were presented along with appropriate least significant difference (LSD) values at a 95 percent confidence level for all possible mean comparisons. Changes in means from C0 to C13 for all measured traits were indicated as total response in units of measure, response per cycle in units of measure calculated as the difference between C0 and C13 means divided by the number of cycles, as a linear response per cycle where appropriate based on the fit of the linear model to the data, and as response per cycle either as a percentage of the C0 mean or as a linear percentage of the intercept, where appropriate.

Mid-parent and high-parent heterosis estimates were expressed in units of measure and as percentages. Heterosis was calculated for each measured trait at each cycle of selection. Inbreeding depression values for grain yield from $F = 0$ to $F = 0.5$ were presented in $q\ ha^{-1}$ and as percentages of the noninbred populations.

For the purposes of comparison to earlier results, and to assist in explanations of unexpected results, several analyses were repeated using data excluding C11 and C13 entries. Analyses of variance and regression analyses for all traits were performed for C0

through C9 entries. Graphical linear trends through C9 were evaluated for traits under selection in FR.

Experiment two

Split-plot analyses of variance, assuming environments, replications, and S_1 lines within populations as random effects and populations as fixed effects, were performed to test the whole-plot effects (populations) and subplot effects (S_1 lines). Significances of environment mean squares were tested with the replications within environment mean squares, while the main effects of populations were tested with population by environment mean squares. Populations by replications within environment mean squares, or error (a), were used for significance testing of population by environment mean squares. Lines within populations and the partitioned effects of lines within each of the four evaluated populations were tested for significance using the appropriate lines within populations by environment mean squares, which in turn were tested with the pooled error term, or error (b). Bartlett's test for homogeneity was used for testing the assumption of homogeneous error variances.

Responses per cycle from C0 to C13 were measured as total responses in units of measure and responses per cycle in units of measure and as percentages of C0 means. Calculations were made for BS10(S_1) and BS11(S_1) populations for all traits measured. All measures represent indirect responses to FR in the inbred *per se* populations.

Shapiro-Wilk (W), skewness, and kurtosis coefficients were used to assess whether the means of random S_1 lines were normally distributed. W values range from zero to one, with values near one resulting in acceptance of the null hypothesis that S_1

lines represent a random sample from a normal distribution. Positive values of skewness suggest elongated upper tails of the distributions, with negative values indicating elongated lower tails. Positive values of kurtosis suggest longer tails than from normal distributions with the same standard deviations, while a negative value indicates a flat-topped characteristic of the distribution.

Variation among random S_1 lines within each population were used for estimation of genotypic and genotype by environment interaction variances and heritabilities for all measured traits, based on expected genotype, genotype by environment, and error mean squares. Genetic variance among random S_1 lines equals $\sigma^2_A + 1/4 \sigma^2_D$ (assuming $p = q$ for the estimate of σ^2_D), and heritability estimates were in the broad sense on an entry mean basis. While variance components and heritabilities were, by definition, positive, estimates for either may be negative. Standard errors of all variance component estimates were calculated as indicated by Hallauer and Miranda-Filho (1988):

$$SE(\sigma^2) = \frac{2}{c^2} \times \left[\frac{MS1^2}{df + 2} + \frac{MS2^2}{df + 2} \right],$$

where c is the coefficient of the variance component as determined by the expected mean squares, and $MS1$ and $MS2$ with their corresponding degrees of freedom (df) are the mean squares for the component of interest and the error mean square with which it was tested. Because variance component estimates do not follow a normal distribution, changes in variance from $C0$ to $C13$ populations were deemed significant when the intervals of a pair of variance estimates determined by the standard errors did not overlap.

While standard errors for variance components were exact, standard errors of heritability estimates were herein calculated using the approximation:

$$SE(h^2) = \frac{SE(\sigma^2_G)}{\left(\frac{\sigma^2}{re}\right) + \left(\frac{\sigma^2_{GE}}{e}\right) + \sigma^2_G}$$

(Hallauer and Miranda-Filho, 1988).

RESULTS

Experiment one

Overall mean grain yield across one Nebraska and six Iowa locations for all population entries was 42.9 q ha⁻¹ (Table 1). Conditions favored fast dry-down for a grain moisture mean of 15.7 percent and a stalk lodging mean of 38.4 percent across six locations. Overall means for non-selected traits were 224.6, 119.9, 81.9, and 84.5 for plant and ear heights in centimeters (cm) and number of days to mid-anthesis and mid-silk, respectively (Table 2). Grain yield means for the check hybrids B77/B73, B79/MO17, and B73/MO17 were 78.5, 85.5 and 72.2 q ha⁻¹, respectively (Table 3), with a mean of 43.2 q ha⁻¹ for the F₂ population of B73/MO17.

Analyses of variance

The combined analyses of variance indicate highly significant differences (probF < 0.01) among environments for grain yield and moisture (Table 4) and root and stalk lodging (Table 5), with significant differences (probF < 0.05) for plant and ear height (Table 6) and days to mid-anthesis and mid-silk (Table 7). As error variances among environments are heterogeneous, F tests for significance of partitioned entry mean squares are tested with the corresponding environment interaction mean square, rather than the entry by environment mean square.

Differences among entries for grain yield are highly significant among entries within BS10, BS10/BS11, BS10(S₁) and (BS10/BS11)(S₁) and among populations, and significant among entries within BS11 and BS11(S₁) (Table 4). Differences within duplicate entries are not significant for grain yield or for any other trait measured. Highly

Table 1. Entry means of maize populations for selected traits combined across environments with overall means, standard errors, and LSD(.05) for mean comparisons.

Population	Grain yield† q ha ⁻¹	Grain moisture† %	Root lodging‡ %	Stalk lodging‡ %
BS10C0	44.59	15.30	1.03	46.36
BS10C0	43.95	15.33	1.38	41.11
BS10(FR)C3	44.13	15.29	1.90	37.94
BS10(FR)C5	48.65	15.51	0.80	47.33
BS10(FR)C7	47.58	14.81	1.33	34.30
BS10(FR)C9	50.84	15.40	0.86	25.60
BS10(FR)C11	59.46	15.69	1.85	33.23
BS10(FR)C13	63.68	15.93	2.22	20.64
BS10(FR)C13	62.98	16.01	1.92	26.28
BS11C0	45.84	17.24	1.71	49.80
BS11C0	48.54	17.16	2.71	47.51
BS11(FR)C3	49.86	16.38	2.16	35.11
BS11(FR)C5	51.09	16.26	2.99	49.94
BS11(FR)C7	52.83	16.06	2.22	42.22
BS11(FR)C9	53.90	16.19	1.64	40.97
BS11(FR)C11	54.75	15.67	1.20	38.08
BS11(FR)C13	54.19	14.54	1.22	41.72
BS11(FR)C13	55.16	14.62	1.50	43.13
BS10C0/BS11C0	47.18	16.28	1.25	48.89
BS10C0/BS11C0	53.99	16.34	1.00	43.94
BS10(FR)C3/BS11(FR)C3	55.98	15.53	2.88	34.88
BS10(FR)C5/BS11(FR)C5	61.50	15.61	2.04	45.32
BS10(FR)C7/BS11(FR)C7	68.66	15.68	2.22	38.28
BS10(FR)C9/BS11(FR)C9	69.93	15.79	1.27	32.11
BS10(FR)C11/BS11(FR)C11	62.44	15.55	1.09	39.19
BS10(FR)C13/BS11(FR)C13	64.24	15.34	1.65	28.80
BS10(FR)C13/BS11(FR)C13	65.31	15.31	0.15	27.24
BS10C0(S1)	24.22	15.62	2.25	41.42
BS10C0(S1)	26.26	15.26	0.64	44.57
BS10(FR)C3(S1)	26.29	15.36	1.12	41.37
BS10(FR)C5(S1)	27.16	15.38	0.82	48.12
BS10(FR)C7(S1)	29.75	15.41	1.59	31.75
BS10(FR)C9(S1)	25.37	14.96	1.01	32.81
BS10(FR)C11(S1)	35.65	15.76	1.24	35.35
BS10(FR)C13(S1)	40.00	15.94	1.35	30.71
BS10(FR)C13(S1)	38.49	15.81	1.50	27.80
BS11C0(S1)	23.96	16.61	3.10	40.16
BS11C0(S1)	26.02	17.07	2.09	40.92
BS11(FR)C3(S1)	29.49	15.88	2.84	33.69
BS11(FR)C5(S1)	31.56	16.26	3.36	51.60
BS11(FR)C7(S1)	27.41	16.14	1.41	40.08
BS11(FR)C9(S1)	28.82	16.05	3.55	41.89
BS11(FR)C11(S1)	32.37	15.47	2.25	35.74
BS11(FR)C13(S1)	31.20	14.72	1.65	35.74

Table 1. (continued)

Population	Grain yield† q ha ⁻¹	Grain moisture† %	Root lodging‡ %	Stalk lodging‡ %
BS11(FR)C13(S1)	30.21	14.79	2.95	40.70
(BS10CO/BS11CO)(S1)	28.10	15.64	0.94	40.21
(BS10CO/BS11CO)(S1)	28.72	15.73	1.60	44.07
(BS10(FR)C3/BS11(FR)C3)(S1)	32.45	15.71	1.39	38.66
(BS10(FR)C5/BS11(FR)C5)(S1)	31.52	14.96	2.79	42.89
(BS10(FR)C7/BS11(FR)C7)(S1)	33.89	15.42	3.82	35.94
(BS10(FR)C9/BS11(FR)C9)(S1)	37.68	15.57	1.72	33.35
(BS10(FR)C11/BS11(FR)C11)(S1)	35.65	15.59	0.73	37.51
(BS10(FR)C13/BS11(FR)C13)(S1)	37.68	15.49	3.24	33.16
(BS10(FR)C13/BS11(FR)C13)(S1)	35.64	15.39	2.48	33.18
Overall means:	42.90	15.68	1.81	38.39
Standard error of an entry mean:	2.17	0.18	0.78	3.57
LSD (0.05) for mean comparisons:	6.02	0.51	2.16	9.91

†Means for grain yield and grain yield represent seven environments

‡Means for root and stalk lodging represent six environments

Table 2. Entry means of maize populations for non-selected traits combined across environments with overall means, standard errors, and LSD(.05) for mean comparisons.

Population	Plant height† cm	Ear height† cm	days to mid-anthesis‡	days to mid-silk‡
BS10C0	231.00	123.50	80.25	83.00
BS10C0	219.00	116.13	81.00	83.50
BS10(FR)C3	217.25	120.00	80.50	83.50
BS10(FR)C5	222.63	119.38	80.00	83.50
BS10(FR)C7	224.75	115.63	82.25	84.50
BS10(FR)C9	226.75	115.75	82.50	84.25
BS10(FR)C11	227.25	121.13	81.00	83.25
BS10(FR)C13	229.75	124.75	80.50	82.50
BS10(FR)C13	225.00	121.13	80.00	82.50
BS11C0	249.00	142.63	84.25	87.75
BS11C0	245.63	140.50	82.50	88.75
BS11(FR)C3	229.75	124.00	82.00	83.50
BS11(FR)C5	232.50	128.63	80.25	82.50
BS11(FR)C7	227.00	116.88	82.00	83.50
BS11(FR)C9	244.38	128.38	80.75	83.50
BS11(FR)C11	236.38	127.00	81.50	83.00
BS11(FR)C13	237.13	124.63	80.75	82.50
BS11(FR)C13	242.25	125.50	81.25	83.25
BS10CO/BS11CO	247.63	137.63	82.50	84.00
BS10CO/BS11CO	242.13	134.75	81.00	84.75
BS10(FR)C3/BS11(FR)C3	233.63	129.50	80.75	82.50
BS10(FR)C5/BS11(FR)C5	236.63	130.13	81.00	83.00
BS10(FR)C7/BS11(FR)C7	243.00	131.38	81.00	83.00
BS10(FR)C9/BS11(FR)C9	240.25	124.38	81.00	82.50
BS10(FR)C11/BS11(FR)C11	231.13	122.63	80.50	82.50
BS10(FR)C13/BS11(FR)C13	236.38	124.38	81.25	82.50
BS10(FR)C13/BS11(FR)C13	233.38	124.25	79.75	81.50
BS10C0(S1)	201.88	105.38	82.50	85.00
BS10C0(S1)	207.88	112.38	81.00	84.75
BS10(FR)C3(S1)	204.63	112.38	81.00	85.25
BS10(FR)C5(S1)	205.88	113.63	83.25	85.50
BS10(FR)C7(S1)	212.75	110.75	83.25	85.75
BS10(FR)C9(S1)	207.38	102.00	82.50	85.50
BS10(FR)C11(S1)	215.88	113.50	83.00	85.25
BS10(FR)C13(S1)	218.38	113.75	82.25	83.25
BS10(FR)C13(S1)	216.13	116.13	82.50	83.75
BS11C0(S1)	216.00	119.63	83.75	89.75
BS11C0(S1)	218.25	122.50	84.25	88.50
BS11(FR)C3(S1)	207.25	106.50	83.00	85.00
BS11(FR)C5(S1)	217.75	121.13	81.75	86.75
BS11(FR)C7(S1)	214.38	113.00	84.75	87.75
BS11(FR)C9(S1)	225.00	119.13	83.00	86.75
BS11(FR)C11(S1)	224.00	117.38	83.25	87.00
BS11(FR)C13(S1)	217.38	110.88	83.00	85.25

Table 2. (continued)

Population	Plant height† cm	Ear height† cm	days to mid-anthesis‡	days to mid-silk‡
BS11(FR)C13(S1)	219.38	111.63	81.75	83.75
(BS10CO/BS11CO)(S1)	212.75	115.75	83.00	87.75
(BS10CO/BS11CO)(S1)	221.50	121.63	82.50	86.75
(BS10(FR)C3/BS11(FR)C3)(S1)	213.25	113.88	82.00	83.50
(BS10(FR)C5/BS11(FR)C5)(S1)	214.38	115.25	81.25	82.50
(BS10(FR)C7/BS11(FR)C7)(S1)	223.50	116.00	82.50	85.00
(BS10(FR)C9/BS11(FR)C9)(S1)	224.50	113.88	82.25	84.75
(BS10(FR)C11/BS11(FR)C11)(S1)	218.25	115.75	83.50	85.50
(BS10(FR)C13/BS11(FR)C13)(S1)	220.25	111.88	81.75	84.75
(BS10(FR)C13/BS11(FR)C13)(S1)	217.88	112.50	82.50	84.00
Overall means:	224.59	119.86	81.91	84.52
Standard error of an entry mean:	3.18	2.89	0.71	0.69
LSD (0.05) for mean comparisons:	8.83	8.00	2.02	1.96

†Plant and ear height means represent four environments.

‡Days to mid-anthesis and mid-silk represent two environments.

Table 3. Means of maize check entries at seven locations and combined across environments for grain yield (YLD), grain moisture (MST), root lodging (RL), stalk lodging (SL), plant height (PH), ear height (EH), and days to mid-anthesis (DTA) and mid-silk (DTS).

Environment	Pedigree	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm	DTA	DTS
Ames	B77/B73	99.34	17.80	0.00	20.00	273.50	149.00	85.50	88.00
	B79/MO17	102.69	17.05	0.00	24.11	231.00	128.50	83.00	85.50
	B73/MO17	86.73	17.60	0.00	38.95	253.00	137.00	84.00	87.00
	(B73/MO17)(S1)	41.67	17.75	0.00	22.93	234.50	125.50	85.50	89.00
Ankeny	B77/B73	76.96	15.55	0.00	2.98	253.00	133.50	80.00	81.00
	B79/MO17	102.12	16.00	0.00	11.97	219.50	126.50	77.00	78.00
	B73/MO17	91.60	14.75	0.00	4.50	238.00	127.50	78.00	80.00
	(B73/MO17)(S1)	44.27	14.80	0.00	7.64	225.00	117.50	80.00	82.00
Carroll	B77/B73	64.19	16.25	2.13	42.18	258.50	138.50	—†	—
	B79/MO17	77.78	16.35	0.00	35.73	224.00	128.00	—	—
	B73/MO17	73.46	16.20	0.00	42.91	245.00	132.00	—	—
	(B73/MO17)(S1)	38.56	16.50	2.04	41.94	232.50	131.00	—	—
Rippey	B77/B73	63.50	14.65	9.34	12.16	255.00	128.50	—	—
	B79/MO17	81.30	15.50	0.00	19.37	227.00	122.00	—	—
	B73/MO17	65.34	14.05	4.53	17.85	243.00	124.50	—	—
	(B73/MO17)(S1)	47.60	14.75	8.53	27.45	224.00	117.00	—	—
Fairfield	B77/B73	77.19	15.20	1.89	54.37	—	—	—	—
	B79/MO17	75.56	15.90	1.73	46.54	—	—	—	—
	B73/MO17	83.12	15.30	3.67	59.79	—	—	—	—
	(B73/MO17)(S1)	47.05	14.80	2.04	57.13	—	—	—	—
Fremont	B77/B73	101.66	15.55	0.00	16.89	—	—	—	—
	B79/MO17	92.84	15.25	0.00	12.84	—	—	—	—
	B73/MO17	82.03	13.70	0.00	6.08	—	—	—	—
	(B73/MO17)(S1)	47.50	14.80	0.00	2.70	—	—	—	—
Crawfordsville	B77/B73	66.79	15.35	—	—	—	—	—	—
	B79/MO17	66.43	16.55	—	—	—	—	—	—
	B73/MO17	58.15	16.45	—	—	—	—	—	—
	(B73/MO17)(S1)	35.67	15.05	—	—	—	—	—	—
Combined	B77/B73	78.52	15.76	2.23	24.76	260.00	137.38	82.75	84.50
	B79/MO17	85.53	16.09	0.29	25.09	225.38	126.25	80.00	81.75
	B73/MO17	77.20	15.44	1.37	28.35	244.75	130.25	81.00	83.50
	(B73/MO17)(S1)	43.19	15.49	2.10	26.63	229.00	122.75	82.75	85.50

† Trait not measured at indicated location

Table 4. Analyses of variance for grain yield and grain moisture combined across seven environments for maize entries.

Source		Grain yield (q ha ⁻¹)		Grain moisture (%)	
		Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment		6	2,962.3 **	6	118.6 **
Replications (Environment)		7	26.5	7	4.5
Entries		53	2,596.2 **	53	4.7 **
BS10		[6]	1,226.8 **	[6]	2.5 **
Linear	{1}		6,399.8 **	{1}	6.1 **
Quadratic	{1}		751.4 *	{1}	4.4 **
Deviations	{4}		52.5	{4}	1.2 **
BS11		[6]	180.7 *	[6]	16.9 **
Linear	{1}		1,030.0 **	{1}	90.2 **
Quadratic	{1}		48.8	{1}	2.2 *
Deviations	{4}		1.3	{4}	2.3 **
BS10/BS11		[6]	959.8 **	[6]	2.6 **
Linear	{1}		3,654.0 **	{1}	10.5 *
Quadratic	{1}		1,453.5 *	{1}	0.7
Deviations	{4}		162.9 **	{4}	1.0 **
BS10(S ₁)		[6]	677.9 **	[6]	1.6 *
Linear	{1}		3,008.2 **	{1}	2.6
Quadratic	{1}		557.2 *	{1}	3.4 **
Deviations	{4}		125.5 *	{4}	0.9
BS11(S ₁)		[6]	136.9 *	[6]	11.2 **
Linear	{1}		455.7	{1}	56.3 **
Quadratic	{1}		69.2	{1}	2.3 *
Deviations	{4}		74.1	{4}	2.2 **
(BS10/BS11)(S ₁)		[6]	231.2 **	[6]	1.0
Linear	{1}		1,205.0 **	{1}	0.4
Quadratic	{1}		57.7	{1}	1.0
Deviations	{4}		31.2	{4}	1.2
Within duplicates		[12]	42.5	[12]	0.2
Among populations		[5]	23,321.7 **	[5]	6.6 **

Table 4. (continued)

Source	Grain yield (q ha ⁻¹)		Grain moisture (%)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	318	65.9	318	0.5 **
BS10 by environment	[36]	90.9 *	[36]	0.2
Linear by environment	{6}	188.6 **	{6}	0.2
Quadratic by environment	{6}	115.0	{6}	0.2
Deviations by environment	{24}	60.4	{24}	0.2
BS11 by environment	[36]	72.4	[36]	0.8 **
Linear by environment	{6}	18.5	{6}	2.8 **
Quadratic by environment	{6}	118.1	{6}	0.4
Deviations by environment	{24}	74.4	{24}	0.4
BS10/BS11 by environment	[36]	52.8	[36]	0.4
Linear by environment	{6}	55.0	{6}	1.0 **
Quadratic by environment	{6}	122.2 *	{6}	0.5
Deviations by environment	{24}	34.9	{24}	0.2
BS10(S ₁) by environment	[36]	38.9	[36]	0.6 **
Linear by environment	{6}	34.7	{6}	1.8 **
Quadratic by environment	{6}	50.5	{6}	0.2
Deviations by environment	{24}	37.0	{24}	0.4
BS11(S ₁) by environment	[36]	45.4	[36]	0.5 *
Linear by environment	{6}	98.7	{6}	0.8 *
Quadratic by environment	{6}	17.0	{6}	0.2
Deviations by environment	{24}	39.2	{24}	0.4
(BS10/BS11)(S ₁) by environment	[36]	32.0	[36]	0.6 **
Linear by environment	{6}	85.1	{6}	0.8 *
Quadratic by environment	{6}	20.8	{6}	0.9 *
Deviations by environment	{24}	21.5	{24}	0.4
Within duplicates by environment	[72]	59.2	[72]	0.3
Among populations by environment	[30]	158.1 **	[30]	0.6 **
Pooled error	366†	55.8	356†	0.3
Total	750†		740†	

†Degrees of freedom adjusted for missing values

Table 5. Analyses of variance for root lodging and stalk lodging combined across six environments for maize entries.

Source	Root lodging (%)		Stalk lodging (%)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment	5	452.7 **	5	50,874.7 **
Replications (Environment)	6	30.4	6	258.2
Entries	53	8.2	53	561.5 **
BS10	[6]	4.1	[6]	1,342.4 **
Linear	{1}	6.8	{1}	5,996.2 **
Quadratic	{1}	5.0	{1}	192.3
Deviations	{4}	3.2	{4}	466.6
BS11	[6]	5.4	[6]	407.7 *
Linear	{1}	17.2	{1}	483.0
Quadratic	{1}	5.2	{1}	172.7
Deviations	{4}	2.4	{4}	447.6
BS10/BS11	[6]	7.9	[6]	878.3 **
Linear	{1}	6.5	{1}	3,508.8 **
Quadratic	{1}	23.8	{1}	31.0
Deviations	{4}	4.3	{4}	432.5
BS10(S ₁)	[6]	1.0	[6]	764.7 **
Linear	{1}	0.0	{1}	3,065.6 *
Quadratic	{1}	1.9	{1}	93.9
Deviations	{4}	1.1	{4}	357.1 *
BS11(S ₁)	[6]	6.5	[6]	405.8
Linear	{1}	1.8	{1}	91.7
Quadratic	{1}	1.4	{1}	247.9
Deviations	{4}	9.0	{4}	523.8 *
(BS10/BS11)(S ₁)	[6]	17.0	[6]	261.0 **
Linear	{1}	14.6	{1}	1,126.9 *
Quadratic	{1}	6.3	{1}	0.2
Deviations	{4}	20.2	{4}	109.7
Within duplicates	[12]	5.0	[12]	75.9
Among populations	[5]	25.1	[5]	897.9 *

Table 5. (continued)

Source	Root lodging (%)		Stalk lodging (%)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	265	7.3	265	153.4 **
BS10 by environment	[30]	6.1	[30]	195.8 *
Linear by environment	{5}	14.0	{5}	369.4 **
Quadratic by environment	{5}	9.2	{5}	131.8
Deviations by environment	{20}	3.3	{20}	168.4
BS11 by environment	[30]	7.2	[30]	148.1
Linear by environment	{5}	16.7 *	{5}	102.0
Quadratic by environment	{5}	7.1	{5}	112.8
Deviations by environment	{20}	4.9	{20}	168.5
BS10/BS11 by environment	[30]	7.2	[30]	180.5 *
Linear by environment	{5}	1.3	{5}	196.9
Quadratic by environment	{5}	24.7 **	{5}	46.3
Deviations by environment	{20}	4.4	{20}	210.0 *
BS10(S ₁) by environment	[30]	4.1	[30]	133.0
Linear by environment	{5}	3.3	{5}	207.7
Quadratic by environment	{5}	7.4	{5}	98.2
Deviations by environment	{20}	3.4	{20}	123.0
BS11(S ₁) by environment	[30]	9.5	[30]	171.7 *
Linear by environment	{5}	2.9	{5}	236.3
Quadratic by environment	{5}	8.0	{5}	94.4
Deviations by environment	{20}	11.6 *	{20}	174.8
(BS10/BS11)(S ₁) by environment	[30]	11.1 *	[30]	72.0
Linear by environment	{5}	5.5	{5}	73.5
Quadratic by environment	{5}	7.4	{5}	54.0
Deviations by environment	{20}	13.4 **	{20}	76.2
Within duplicates by environment	[60]	4.4	[60]	109.4
Among populations by environment	[25]	12.6 **	[25]	281.8 **
Pooled error	318	6.6	318	111.5
Total	647		647	

Table 6. Analyses of variance for plant height and ear height combined across four environments for maize entries.

Source	Plant height (cm)		Ear height (cm)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment	3	5,516.4 *	3	3,584.4 *
Replications (Environment)	4	750.8	4	468.7
Entries	53	1,133.5 **	53	567.1 **
BS10	[6]	113.2	[6]	73.9
Linear	{1}	222.8	{1}	45.5
Quadratic	{1}	106.3	{1}	232.7
Deviations	{4}	87.5	{4}	41.3
BS11	[6]	588.4 **	[6]	696.4 **
Linear	{1}	134.8	{1}	1,720.1 **
Quadratic	{1}	1,692.5 **	{1}	1,339.4
Deviations	{4}	425.7 **	{4}	279.7 *
BS10/BS11	[6]	282.6 *	[6]	288.0 **
Linear	{1}	706.4	{1}	1,471.4 *
Quadratic	{1}	21.9	{1}	35.0
Deviations	{4}	241.8	{4}	55.4
BS10(S _i)	[6]	336.6 **	[6]	181.4 *
Linear	{1}	1,634.5 **	{1}	130.4 *
Quadratic	{1}	99.8	{1}	62.8
Deviations	{4}	71.4	{4}	223.8 *
BS11(S _i)	[6]	286.4 **	[6]	310.7 **
Linear	{1}	364.2	{1}	301.5
Quadratic	{1}	7.1	{1}	1.3
Deviations	{4}	336.8 **	{4}	390.3 **
(BS10/BS11)(S _i)	[6]	146.7	[6]	62.6
Linear	{1}	167.3	{1}	246.1
Quadratic	{1}	30.2	{1}	3.4
Deviations	{4}	170.7	{4}	31.5
Within duplicates	[12]	125.3	[12]	59.8
Among populations	[5]	9,609.6 **	[5]	3,932.0 **

Table 6. (continued)

Source	Plant height (cm)		Ear height (cm)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	159	81.1	159	66.7 *
BS10 by environment	[18]	93.1	[18]	53.6
Linear by environment	{3}	198.8	{3}	86.5
Quadratic by environment	{3}	141.0	{3}	74.2
Deviations by environment	{12}	54.7	{12}	40.2
BS11 by environment	[18]	59.2	[18]	91.3 *
Linear by environment	{3}	61.4	{3}	29.9
Quadratic by environment	{3}	44.5	{3}	208.9 **
Deviations by environment	{12}	62.4	{12}	77.2
BS10/BS11 by environment	[18]	81.5	[18]	61.7
Linear by environment	{3}	104.8	{3}	75.3
Quadratic by environment	{3}	43.8	{3}	20.6
Deviations by environment	{12}	85.2	{12}	68.6
BS10(S _i) by environment	[18]	80.1	[18]	47.4
Linear by environment	{3}	31.5	{3}	4.2
Quadratic by environment	{3}	55.2	{3}	31.6
Deviations by environment	{12}	98.4	{12}	62.1
BS11(S _i) by environment	[18]	48.0	[18]	44.2
Linear by environment	{3}	32.3	{3}	88.5
Quadratic by environment	{3}	59.0	{3}	20.7
Deviations by environment	{12}	49.2	{12}	39.0
(BS10/BS11)(S _i) by environment	[18]	126.7	[18]	85.0 *
Linear by environment	{3}	187.2	{3}	42.0
Quadratic by environment	{3}	143.9	{3}	195.3 **
Deviations by environment	{12}	107.4	{12}	68.2
Within duplicates by environment	[36]	97.6	[36]	74.9 *
Among populations by environment	[15]	39.3	[15]	67.0
Pooled error	212	90.9	212	49.9
Total	431		431	

Table 7. Analyses of variance for days to mid-anthesis and mid-silk combined across two environments for maize entries.

Source	Days to mid-anthesis		Days to mid-silk	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment	1	1,849.2 *	1	2,166.0 *
Replications (Environment)	2	58.1	2	104.2
Entries	53	5.7 **	53	14.3 **
BS10	[6]	4.2	[6]	2.4
Linear	{1}	0.2	{1}	1.3
Quadratic	{1}	7.0	{1}	9.6 *
Deviations	{4}	4.6	{4}	0.9
BS11	[6]	6.5	[6]	28.1 **
Linear	{1}	20.6	{1}	100.3
Quadratic	{1}	7.8	{1}	45.4 *
Deviations	{4}	2.7	{4}	5.7
BS10/BS11	[6]	1.3	[6]	4.3 *
Linear	{1}	5.9	{1}	20.1
Quadratic	{1}	0.3	{1}	1.3
Deviations	{4}	0.4	{4}	1.1
BS10(S _i)	[6]	3.1	[6]	3.7
Linear	{1}	4.4	{1}	5.2
Quadratic	{1}	3.7	{1}	14.5
Deviations	{4}	2.6	{4}	0.7
BS11(S _i)	[6]	4.8	[6]	17.0 *
Linear	{1}	6.0	{1}	52.2
Quadratic	{1}	0.0	{1}	0.0
Deviations	{4}	5.7	{4}	12.5 *
(BS10/BS11)(S _i)	[6]	2.1	[6]	13.1 *
Linear	{1}	0.0	{1}	13.5
Quadratic	{1}	1.1	{1}	25.3
Deviations	{4}	2.8 **	{4}	10.0
Within duplicates	{12}	2.3	{12}	1.5
Among populations	{5}	28.5 *	{5}	65.4 **

Table 7. (continued)

Source	Days to mid-anthesis		Days to mid-silk	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	53	2.0	53	1.9
BS10 by environment	[6]	2.5	[6]	2.8
Linear by environment	{1}	1.0	{1}	0.0
Quadratic by environment	{1}	0.1	{1}	0.0
Deviations by environment	{4}	3.5	{4}	4.1
BS11 by environment	[6]	2.4	[6]	1.2
Linear by environment	{1}	2.9	{1}	3.3
Quadratic by environment	{1}	2.5	{1}	0.2
Deviations by environment	{4}	2.2	{4}	1.0
BS10/BS11 by environment	[6]	0.8	[6]	1.0
Linear by environment	{1}	0.1	{1}	1.4
Quadratic by environment	{1}	0.4	{1}	0.1
Deviations by environment	{4}	1.1	{4}	1.1
BS10(S _i) by environment	[6]	1.2	[6]	0.5
Linear by environment	{1}	1.4	{1}	1.4
Quadratic by environment	{1}	0.2	{1}	0.9
Deviations by environment	{4}	1.4	{4}	0.1
BS11(S _i) by environment	[6]	3.5	[6]	3.0
Linear by environment	{1}	9.7 *	{1}	3.3
Quadratic by environment	{1}	0.1	{1}	8.4
Deviations by environment	{4}	2.8	{4}	1.6
(BS10/BS11)(S _i) by environment	[6]	0.8	[6]	2.3
Linear by environment	{1}	3.2	{1}	0.2
Quadratic by environment	{1}	1.2	{1}	1.1
Deviations by environment	{4}	0.2	{4}	3.1
Within duplicates by environment	[12]	1.0	[12]	1.8
Among populations by environment	[5]	5.6 *	[5]	3.0
Pooled error	106	1.8	106	2.6
Total	215		215	

significant differences are present among entries and for entries within BS10, BS11, BS10/BS11, and BS11(S₁), and among populations. Significant differences exist for grain moisture among entries within BS10(S₁).

Root lodging mean squares for entries, including entries among and within all populations, are not significant (Table 5). Regression coefficients for root lodging, therefore, are not estimated. Highly significant differences among entries for stalk lodging include the overall entry mean square and within BS10, BS10/BS11, BS10(S₁), and (BS10/BS11)(S₁) populations. Significant stalk lodging differences exist for entries within BS11.

Differences among entries within BS11 and BS11(S₁) and among populations for plant and ear heights, and within BS10(S₁) for plant height and BS10/BS11 for ear height are highly significant (Table 6). Differences within BS10/BS11 for plant height and BS10(S₁) for ear height are significant at the 0.05 level. Only the overall entry mean square at the 0.01 level and among population mean square at the 0.05 level are significant for days to mid-anthesis (Table 7). Entries, entries within BS11, and entries among populations show highly significant differences for days to mid-silk, with significant differences for entries within BS10/BS11, BS11(S₁), and (BS10/BS11)(S₁).

Entries by environment interaction mean squares are highly significant for grain moisture and stalk lodging and significant for ear height (Tables 4, 5, 6, and 7). Highly significant entry by environment mean squares include within BS11, BS10(S₁), and (BS10/BS11)(S₁) for grain moisture. Significant entry by environment mean squares include within BS10 for grain yield, BS11(S₁) for grain moisture, (BS10/BS11)(S₁) for

root lodging, BS10, BS10/BS11, and BS11(S₁) for stalk lodging, and BS11 and (BS10/BS11)(S₁) for ear height.

Direct changes associated with selection

Significant improvements based on LSD (0.05) values in the population cross, the direct unit of selection, have been made during 13 cycles of selection for the selected traits grain yield, grain moisture, and stalk lodging (Tables 8 and 9), and for the non-selected traits plant and ear height and days to mid-anthesis and mid-silk (Tables 10 and 11). Responses per cycle as a percentage of the C₀ population mean and as a linear response per cycle, where appropriate as determined by the significance (probF < 0.05) of linear, quadratic, and deviation mean squares, are presented in Table 12. Regression coefficients significant at probF < 0.05 are presented along with R² values (Table 13). Cycle-to-cycle trends for selected traits, with the exception of root lodging, are shown in Figures 1 through 6. Best-fit linear trends, regardless of the linearity of the data, are shown in Figures 7 through 20 for seven traits.

Improvement for grain yield in the population cross, the direct unit of selection, does not fit a linear model (Table 4). While the linear mean square is significant, significant quadratic and deviation mean squares indicate a non-linear response over 13 selection cycles. Improvements from C₀ to C₉ are followed by a significant (probF < 0.05) (Table 8) decrease from C₉ to C₁₁. Overall grain yield response as a percentage of the C₀ mean is equal to 2.2 percent in this study. A linear response of 2.2 percent per cycle is evident for the inbred population cross, from 28.4 q ha⁻¹ at C₀ to 36.7 at C₁₃

Table 8. Noninbred maize population means for grain yield (YLD) and moisture (MST) across seven locations, and for root lodging (RL) and stalk lodging (SL) across six locations, shown with standard errors of means and LSDs(0.05) for mean comparisons.

Population	YLD q ha ⁻¹	MST %	RL %	SL %
BS10C0+	44.27	15.31	1.20	43.73
BS10(FR)C3	44.13	15.29	1.90	37.94
BS10(FR)C5	48.65	15.51	0.80	47.33
BS10(FR)C7	47.58	14.81	1.33	34.30
BS10(FR)C9	50.84	15.40	0.86	25.60
BS10(FR)C11	59.46	15.69	1.85	33.23
BS10(FR)C13+	63.33	15.97	2.07	23.46
Standard error of C0 or C13 mean	1.80	0.09	0.50	2.86
Standard error of C3, C5, C7, C9 or C11 mean	2.55	0.13	0.71	4.04
LSD(.05) for C0 vs C13 mean	5.17	0.26	1.45	8.25
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	6.33	0.31	1.78	10.10
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	7.31	0.36	2.05	11.67
BS11C0+	47.19	17.20	2.21	48.66
BS11(FR)C3	49.86	16.38	2.16	35.11
BS11(FR)C5	51.09	16.26	2.99	49.94
BS11(FR)C7	52.83	16.06	2.22	42.22
BS11(FR)C9	53.90	16.19	1.64	40.97
BS11(FR)C11	54.75	15.67	1.20	38.08
BS11(FR)C13+	54.67	14.58	1.36	42.42
Standard error of C0 or C13 mean	1.61	0.17	0.55	2.48
Standard error of C3, C5, C7, C9 or C11 mean	2.27	0.24	0.78	3.51
LSD(.05) for C0 vs C13 mean	4.61	0.48	1.59	7.17
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	5.65	0.59	1.94	8.79
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	6.52	0.68	2.24	10.15
BS10C0/BS11C0+	50.59	16.31	1.13	46.42
BS10(FR)C3/BS11(FR)C3	55.98	15.53	2.88	34.88
BS10(FR)C5/BS11(FR)C5	61.50	15.61	2.04	45.32
BS10(FR)C7/BS11(FR)C7	68.66	15.68	2.22	38.28
BS10(FR)C9/BS11(FR)C9	69.93	15.79	1.27	32.11
BS10(FR)C11/BS11(FR)C11	62.44	15.55	1.09	39.19
BS10(FR)C13/BS11(FR)C13+	64.78	15.33	0.90	28.02
Standard error of C0 or C13 mean	1.37	0.11	0.55	2.74
Standard error of C3, C5, C7, C9 or C11 mean	1.94	0.16	0.78	3.88
LSD(.05) for C0 vs C13 mean	3.94	0.33	1.59	7.92
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	4.82	0.40	1.94	9.70
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	5.57	0.46	2.24	11.20

+Cycle 0 and cycle 13 populations were replicated four times at each location, with two replications at each location for all other populations.

Table 9. Inbred maize population means for grain yield (YLD) and moisture (MST) across seven locations, and for root lodging (RL) and stalk lodging (SL) across six locations, shown with standard errors of means and LSDs(0.05) for mean comparisons.

Population	YLD q ha ⁻¹	MST %	RL %	SL %
BS10C0†	25.24	15.44	1.45	42.99
BS10(FR)C3	26.29	15.36	1.12	41.37
BS10(FR)C5	27.16	15.38	0.82	48.12
BS10(FR)C7	29.75	15.41	1.59	31.75
BS10(FR)C9	25.37	14.96	1.01	32.81
BS10(FR)C11	35.65	15.76	1.24	35.35
BS10(FR)C13†	39.24	15.88	1.42	29.25
Standard error of C0 or C13 mean	1.18	0.15	0.41	2.35
Standard error of C3, C5, C7, C9 or C11 mean	1.67	0.21	0.58	3.33
LSD(.05) for C0 vs C13 mean	3.38	0.42	1.19	6.80
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	4.14	0.52	1.46	8.33
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	4.78	0.60	1.68	9.61
BS11C0†	24.99	16.84	2.60	40.54
BS11(FR)C3	29.49	15.88	2.84	33.69
BS11(FR)C5	31.56	16.26	3.36	51.60
BS11(FR)C7	27.41	16.14	1.41	40.08
BS11(FR)C9	28.82	16.05	3.55	41.89
BS11(FR)C11	32.37	15.47	2.25	35.74
BS11(FR)C13†	30.70	14.75	2.30	38.22
Standard error of C0 or C13 mean	1.27	0.13	0.63	2.67
Standard error of C3, C5, C7, C9 or C11 mean	1.80	0.18	0.89	3.78
LSD(.05) for C0 vs C13 mean	3.65	0.37	1.82	7.72
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	4.47	0.45	2.23	9.46
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	5.17	0.52	2.58	10.92
BS10C0/BS11C0†	28.41	15.69	1.27	42.14
BS10(FR)C3/BS11(FR)C3	32.45	15.71	1.39	38.66
BS10(FR)C5/BS11(FR)C5	31.52	14.96	2.79	42.89
BS10(FR)C7/BS11(FR)C7	33.89	15.42	3.82	35.94
BS10(FR)C9/BS11(FR)C9	37.68	15.57	1.72	33.35
BS10(FR)C11/BS11(FR)C11	35.65	15.59	0.73	37.51
BS10(FR)C13/BS11(FR)C13†	36.66	15.44	2.86	33.17
Standard error of C0 or C13 mean	1.07	0.14	0.68	1.73
Standard error of C3, C5, C7, C9 or C11 mean	1.51	0.20	0.96	2.45
LSD(.05) for C0 vs C13 mean	3.07	0.41	1.96	5.00
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	3.75	0.51	2.41	6.13
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	4.34	0.58	2.78	7.08

†Cycle 0 and cycle 13 populations were replicated four times at each location, with two replications at each location for all other populations.

Table 10. Noninbred maize population means for plant height (PH) and ear height (EH) across four locations, and for days to mid-anthesis (DTA) and mid-silk (DTS) across two locations, shown with standard errors of means and LSDs(0.05) for mean comparisons.

Population	PH cm	EH cm	DTA	DTS
BS10C0+	225.00	119.81	80.63	83.25
BS10(FR)C3	217.25	120.00	80.50	83.50
BS10(FR)C5	222.63	119.38	80.00	83.50
BS10(FR)C7	224.75	115.63	82.25	84.50
BS10(FR)C9	226.75	115.75	82.50	84.25
BS10(FR)C11	227.25	121.13	81.00	83.25
BS10(FR)C13+	227.38	122.94	80.25	82.50
Standard error of C0 or C13 mean	2.41	1.83	0.56	0.59
Standard error of C3, C5, C7, C9 or C11 mean	3.41	2.59	0.80	0.83
LSD(.05) for C0 vs C13 mean	7.17	5.44	1.95	2.03
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	8.78	6.66	2.39	2.49
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	10.14	7.69	2.76	2.87
BS11C0+	247.31	141.56	83.38	88.25
BS11(FR)C3	229.75	124.00	82.00	83.50
BS11(FR)C5	232.50	128.63	80.25	82.50
BS11(FR)C7	227.00	116.88	82.00	83.50
BS11(FR)C9	244.38	128.38	80.75	83.50
BS11(FR)C11	236.38	127.00	81.50	83.00
BS11(FR)C13+	239.69	125.06	81.00	82.88
Standard error of C0 or C13 mean	1.92	2.39	0.55	0.39
Standard error of C3, C5, C7, C9 or C11 mean	2.72	3.38	0.77	0.55
LSD(.05) for C0 vs C13 mean	5.72	7.10	1.89	1.36
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	7.00	8.69	2.32	1.66
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	8.09	10.04	2.68	1.92
BS10C0/BS11C0+	244.88	136.19	81.75	84.38
BS10(FR)C3/BS11(FR)C3	233.63	129.50	80.75	82.50
BS10(FR)C5/BS11(FR)C5	236.63	130.13	81.00	83.00
BS10(FR)C7/BS11(FR)C7	243.00	131.38	81.00	83.00
BS10(FR)C9/BS11(FR)C9	240.25	124.38	81.00	82.50
BS10(FR)C11/BS11(FR)C11	231.13	122.63	80.50	82.50
BS10(FR)C13/BS11(FR)C13+	234.88	124.31	80.50	82.00
Standard error of C0 or C13 mean	2.26	1.96	0.31	0.35
Standard error of C3, C5, C7, C9 or C11 mean	3.19	2.78	0.44	0.49
LSD(.05) for C0 vs C13 mean	6.71	5.84	1.09	1.21
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	8.22	7.15	1.33	1.48
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	9.49	8.25	1.54	1.71

+Cycle 0 and cycle 13 populations were replicated four times at each location, with two replications at each location for all other populations.

Table 11. Inbred maize population means for plant height (PH) and ear height (EH) across four locations, and for days to mid-anthesis (DTA) and mid-silk (DTS) across two locations, shown with standard errors of means and LSDs(0.05) for mean comparisons.

Population	PH cm	EH cm	DTA	DTS
BS10C0+	204.88	108.88	81.75	84.88
BS10(FR)C3	204.63	112.38	81.00	85.25
BS10(FR)C5	205.88	113.63	83.25	85.50
BS10(FR)C7	212.75	110.75	83.25	85.75
BS10(FR)C9	207.38	102.00	82.50	85.50
BS10(FR)C11	215.88	113.50	83.00	85.25
BS10(FR)C13+	217.25	114.94	82.38	83.50
Standard error of C0 or C13 mean	2.24	1.72	0.38	0.24
Standard error of C3, C5, C7, C9 or C11 mean	3.16	2.43	0.54	0.35
LSD(.05) for C0 vs C13 mean	6.65	5.11	1.33	0.85
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	8.14	6.26	1.63	1.04
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	9.40	7.23	1.88	1.20
BS11C0+	217.13	121.06	84.00	89.13
BS11(FR)C3	207.25	106.50	83.00	85.00
BS11(FR)C5	217.75	121.13	81.75	86.75
BS11(FR)C7	214.38	113.00	84.75	87.75
BS11(FR)C9	225.00	119.13	83.00	86.75
BS11(FR)C11	224.00	117.38	83.25	87.00
BS11(FR)C13+	218.38	111.25	82.38	84.50
Standard error of C0 or C13 mean	1.73	1.66	0.66	0.61
Standard error of C3, C5, C7, C9 or C11 mean	2.45	2.35	0.94	0.87
LSD(.05) for C0 vs C13 mean	5.15	4.94	2.29	2.12
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	6.30	6.05	2.81	2.60
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	7.28	6.99	3.24	3.00
BS10C0/BS11C0+	217.13	118.69	82.75	87.25
BS10(FR)C3/BS11(FR)C3	213.25	113.88	82.00	83.50
BS10(FR)C5/BS11(FR)C5	214.38	115.25	81.25	82.50
BS10(FR)C7/BS11(FR)C7	223.50	116.00	82.50	85.00
BS10(FR)C9/BS11(FR)C9	224.50	113.88	82.25	84.75
BS10(FR)C11/BS11(FR)C11	218.25	115.75	83.50	85.50
BS10(FR)C13/BS11(FR)C13+	219.06	112.19	82.13	84.38
Standard error of C0 or C13 mean	2.81	2.31	0.33	0.54
Standard error of C3, C5, C7, C9 or C11 mean	3.98	3.26	0.46	0.76
LSD(.05) for C0 vs C13 mean	8.36	6.85	1.13	1.85
LSD(.05) for C0 or C13 vs C3, C5, C7, C9, or C11 mean	10.24	8.39	1.38	2.27
LSD(.05) for comparing C3, C5, C7, C9, or C11 means	11.83	9.69	1.60	2.62

+Cycle 0 and cycle 13 populations were replicated four times at each location, with two replications at each location for all other populations.

Table 12. Response for eight maize traits to 13 cycles of selection shown in actual units. Linear responses are shown where the linear mean squares are significant and the quadratic and deviations mean squares are not significant.

Trait	Population	Response (C0 to C13) (Units)	Response per cycle (C13-C0)/13 (Units)	Response per cycle Linear (Units)	Response per cycle CO to C13 (% of CO mean)	Response per cycle Linear (% of intercept)
Grain yield (q ha⁻¹)						
	BS10	19.066	1.467		3.313	
	BS11	7.484	0.576	0.593	1.220	1.241
	BS10/BS11	14.191	1.092		2.158	
	BS10(S1)	14.008	1.078		4.270	
	BS11(S1)	5.710	0.439		1.758	
	(BS10/BS11)(S1)	8.251	0.635	0.641	2.234	2.200
Grain moisture (%)						
	BS10	0.657	0.051		0.330	
	BS11	-2.618	-0.201		-1.171	
	BS10/BS11	-0.986	-0.076		-0.465	
	BS10(S1)	0.439	0.034		0.219	
	BS11(S1)	-2.089	-0.161		-0.954	
	(BS10/BS11)(S1)	-0.246	-0.019		-0.121	
Root lodging (%)						
	BS10	0.868	0.067		5.556	
	BS11	-0.850	-0.065		-2.961	
	BS10/BS11	-0.226	-0.017		-1.546	
	BS10(S1)	-0.024	-0.002		-0.126	
	BS11(S1)	-0.300	-0.023		-0.890	
	(BS10/BS11)(S1)	1.594	0.123		9.675	
Stalk lodging (%)						
	BS10	-20.276	-1.560	-1.544	-3.566	-3.414
	BS11	-6.234	-0.480		-0.986	
	BS10/BS11	-18.397	-1.415	-1.181	-3.049	-2.588
	BS10(S1)	-13.740	-1.057		-2.458	
	BS11(S1)	-2.321	-0.179		-0.440	
	(BS10/BS11)(S1)	-8.972	-0.690	-0.669	-1.638	-1.585

Table 12. (continued)

Trait	Population	Response (C0 to C13) (Units)	Response per cycle (C13-C0)/13 (Units)	Response per cycle Linear (Units)	Response per cycle C0 to C13 (% of C0 mean)	Response per cycle Linear (% of intercept)
Plant height (cm)						
	BS10	2.375	0.183		0.081	
	BS11	-7.625	-0.587		-0.237	
	BS10/BS11	-10.000	-0.769		-0.314	
	BS10(S1)	12.375	0.952	0.987	0.465	0.485
	BS11(S1)	1.250	0.096		0.044	
	(BS10/BS11)(S1)	1.938	0.149		0.069	
Ear height (cm)						
	BS10	3.125	0.240		0.201	
	BS11	-16.500	-1.269		-0.897	
	BS10/BS11	-11.875	-0.913	-0.937	-0.671	-0.693
	BS10(S1)	6.063	0.466		0.428	
	BS11(S1)	-9.813	-0.755		-0.623	
	(BS10/BS11)(S1)	-6.500	-0.500		-0.421	
Days to mid-anthesis						
	BS10	-0.375	-0.029		-0.036	
	BS11	-2.375	-0.183		-0.219	
	BS10/BS11	-1.250	-0.096		-0.118	
	BS10(S1)	0.625	0.048		0.059	
	BS11(S1)	-1.625	-0.125		-0.149	
	(BS10/BS11)(S1)	-0.625	-0.048		-0.058	
Days to mid-silk						
	BS10	-0.750	-0.058		-0.069	
	BS11	-5.375	-0.413		-0.469	
	BS10/BS11	-2.375	-0.183		-0.217	
	BS10(S1)	-1.375	-0.106		-0.125	
	BS11(S1)	-4.625	-0.356		-0.399	
	(BS10/BS11)(S1)	-2.875	-0.221		-0.253	

Table 13. Regression coefficients with standard errors, and R^2 parameters for selection response of five maize traits† to 13 cycles of selection. Parameters for which mean squares are not significant are not shown.

Population	Parameter	Grain yield q ha ⁻¹	Grain moisture %	Stalk lodging %	Plant height cm	Ear height cm
BS10	b ₀	44.360±1.084	15.365±0.159	45.219±3.081		
	b ₁	-0.314±0.407	-0.091±0.060	-1.544±0.370		
	b ₂	0.138±0.030	0.011±0.004			
	R ²	0.971	0.694 ‡	0.713		
BS11	b ₀	47.779±0.613	17.061±0.225			135.546±3.824
	b ₁	0.593±0.074	-0.079±0.084			-1.013±0.460
	b ₂		-0.007±0.006			
	R ²	.902	0.909 ‡			0.410 ‡
BS10/BS11	b ₀	49.832±2.315	16.121±0.127	45.633±2.750		135.127±1.308
	b ₁	3.607±0.870	-0.060±0.015	-1.181±0.330		-0.937±0.157
	b ₂	-0.191±0.064				
	R ²	0.838 ‡	0.686 ‡	0.646		0.835
BS10(S1)	b ₀	25.737±1.725		44.582±2.534	203.391±1.800	109.207±2.634
	b ₁	-0.530±0.648		-1.104±0.305	0.987±0.216	0.279±0.317
	b ₂	0.119±0.048				
	R ²	0.867 ‡		0.653 ‡	0.748	.100 ‡
BS11(S1)	b ₀		16.683±0.234			
	b ₁		-0.040±0.088			
	b ₂		-0.008±0.007			
	R ²		0.853 ‡			
(BS10/BS11)(S1)	b ₀	29.136±0.850		42.200±1.441		
	b ₁	0.641±0.102		-0.669±0.173		
	b ₂					
	R ²	0.849		0.681		

† No parameters for root lodging or days to mid-anthesis or mid-silk were significant. These traits are not shown.

‡ Deviation mean squares are significant.

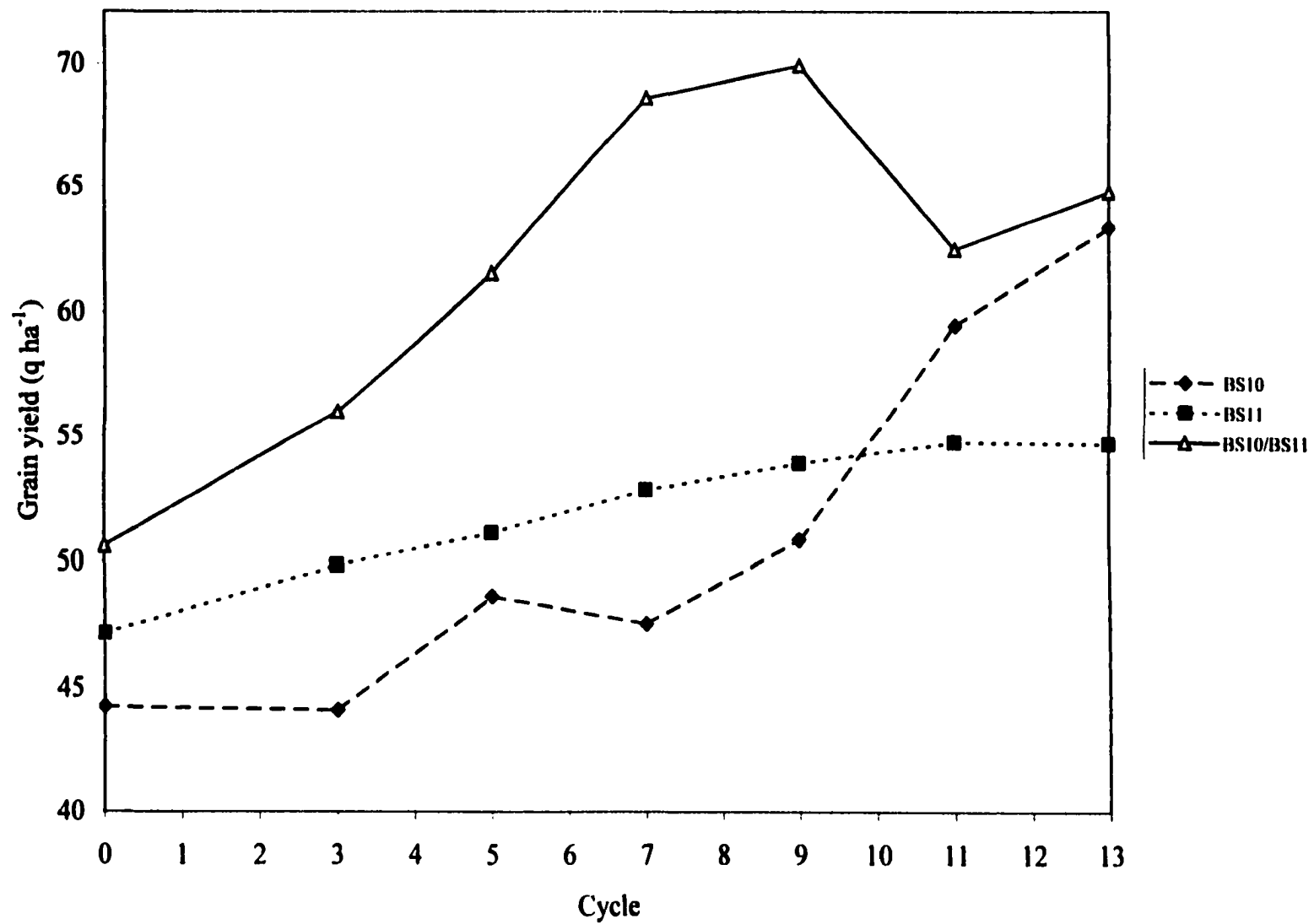


Figure 1. Noninbred maize population response for grain yield through 13 cycles of selection.

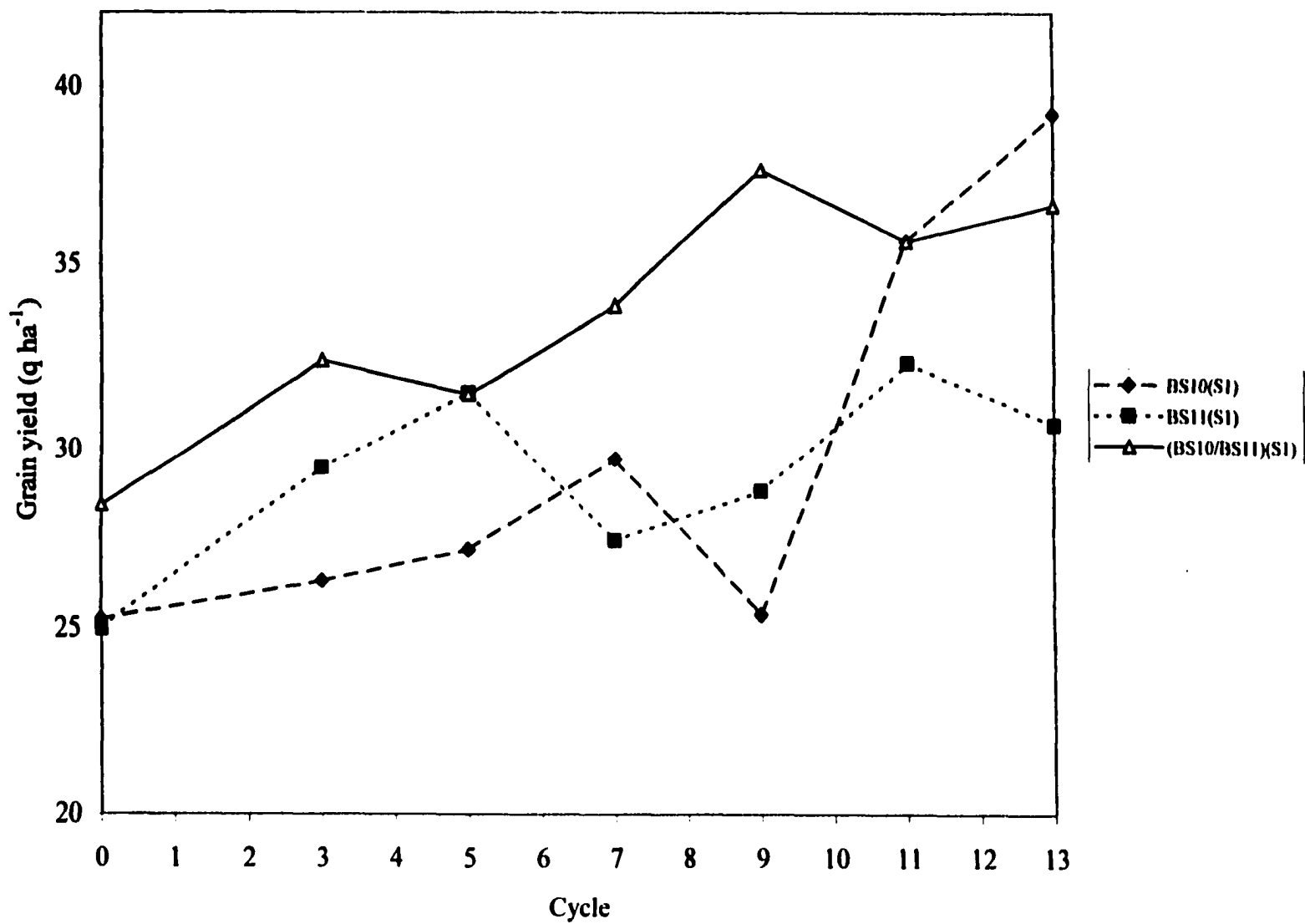


Figure 2. Inbred maize population response for grain yield through 13 cycles of selection.

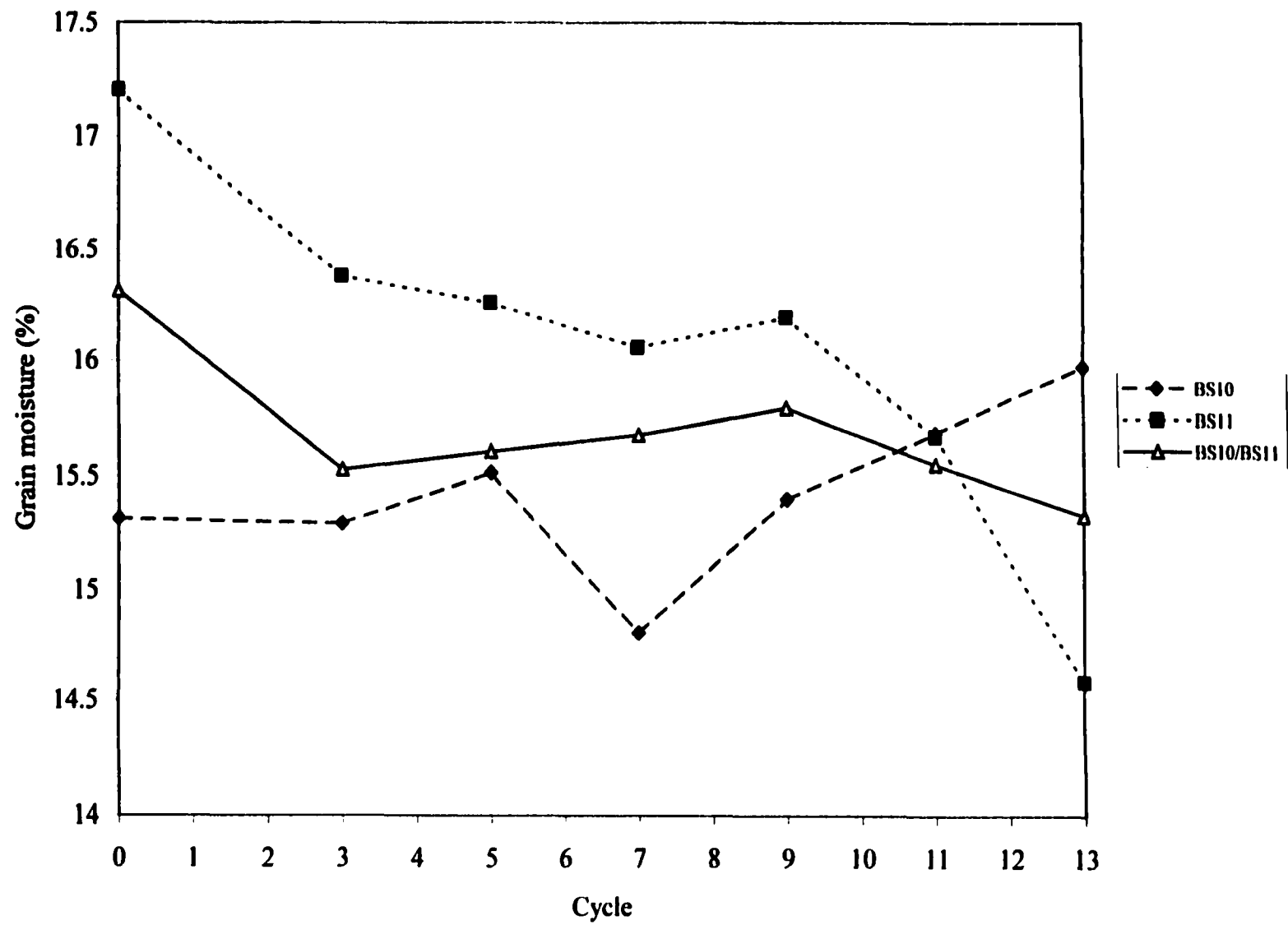


Figure 3. Noninbred maize population response for grain moisture through 13 cycles of selection.

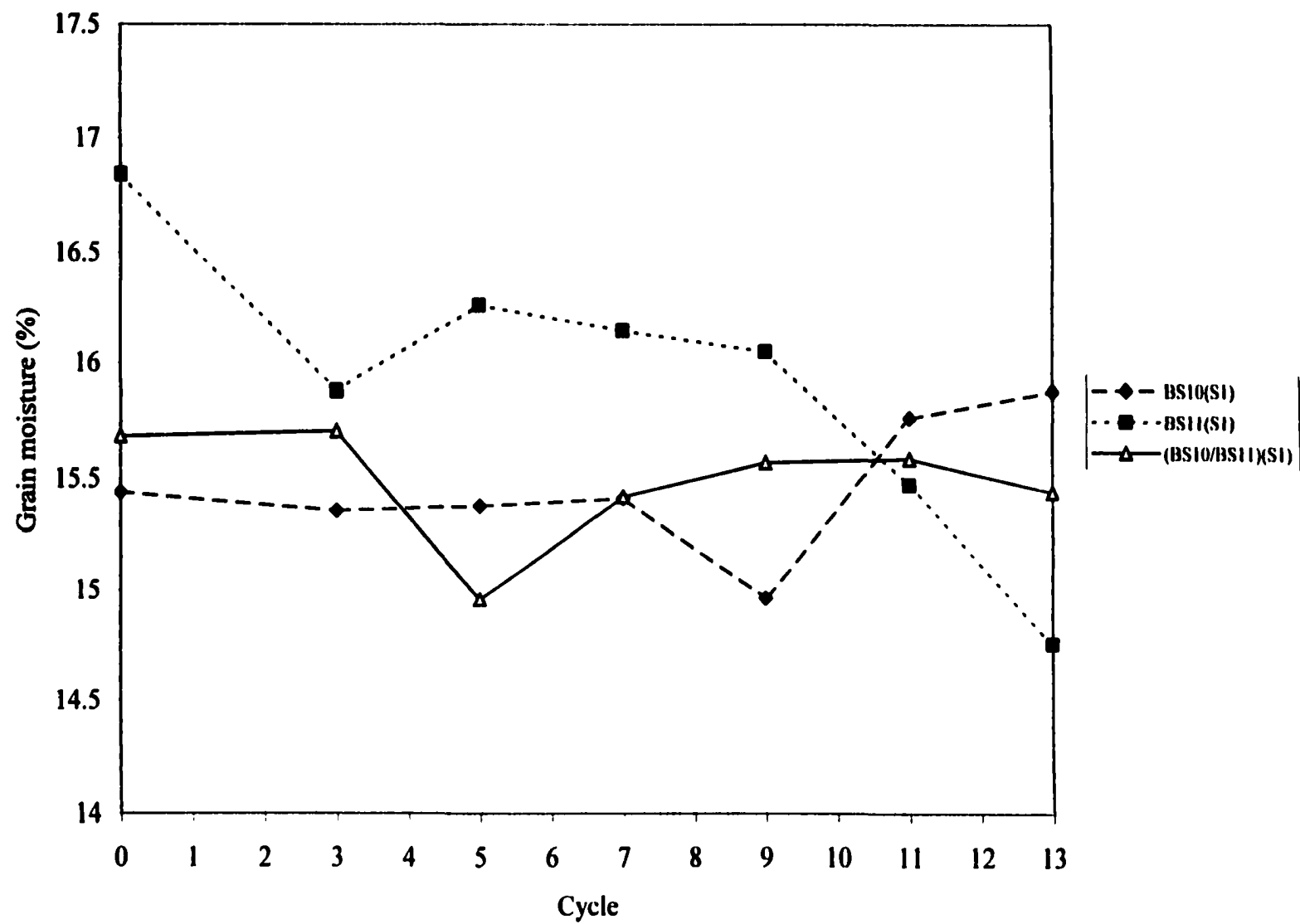


Figure 4. Inbred maize population response for grain moisture through 13 cycles of selection.

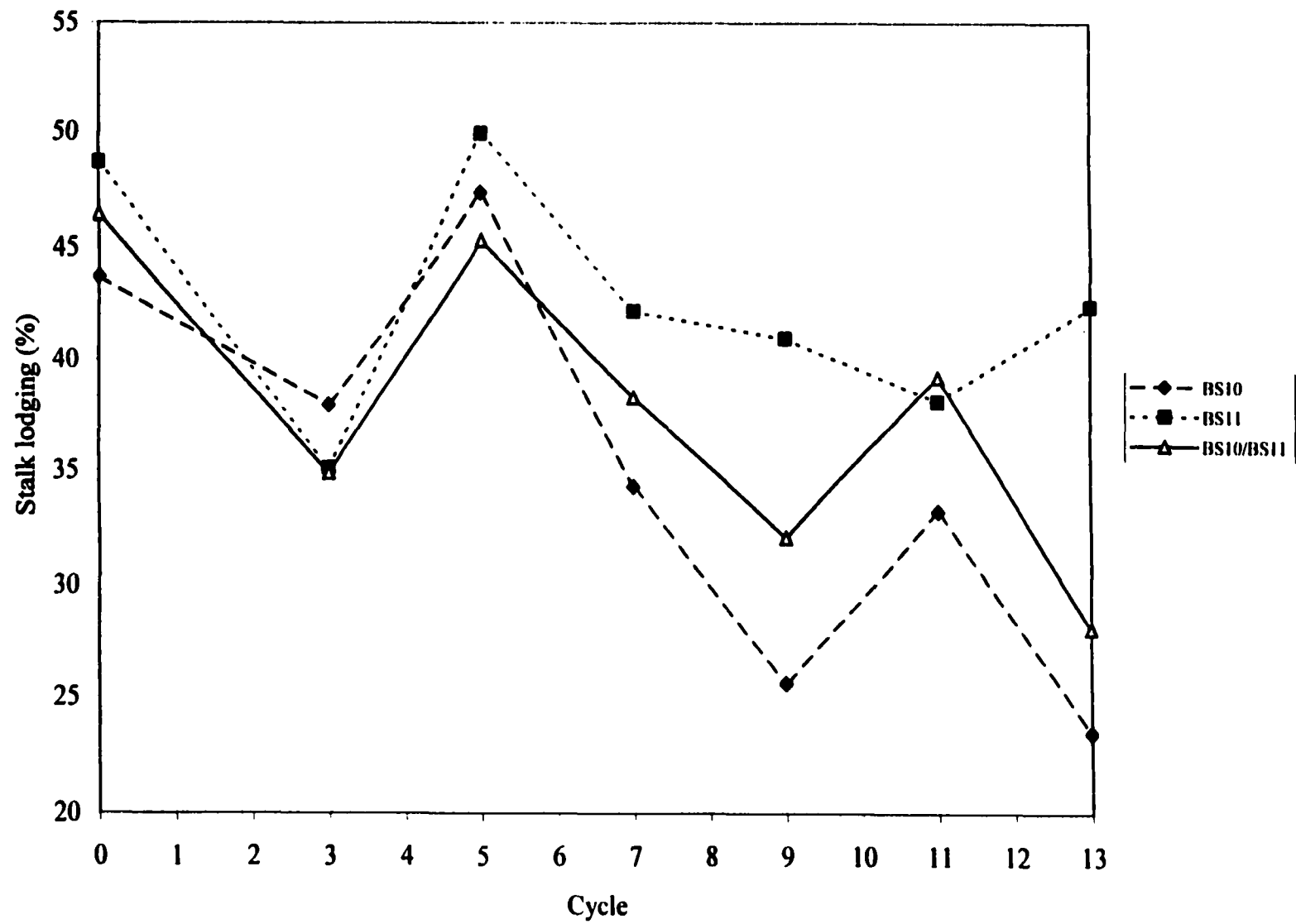


Figure 5. Noninbred maize population response for stalk lodging through 13 cycles of selection.

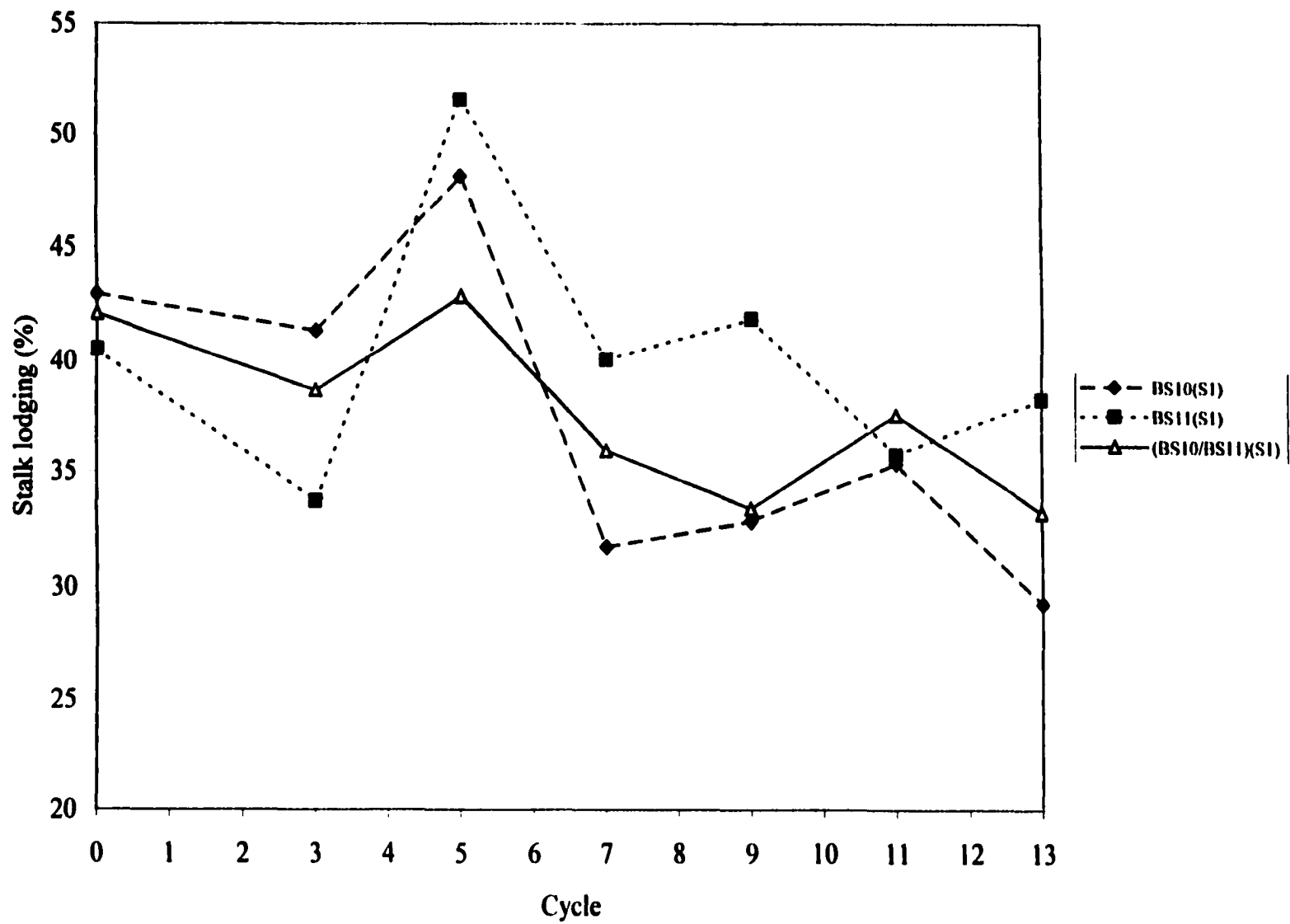


Figure 6. Inbred maize population response for stalk lodging through 13 cycles of selection.

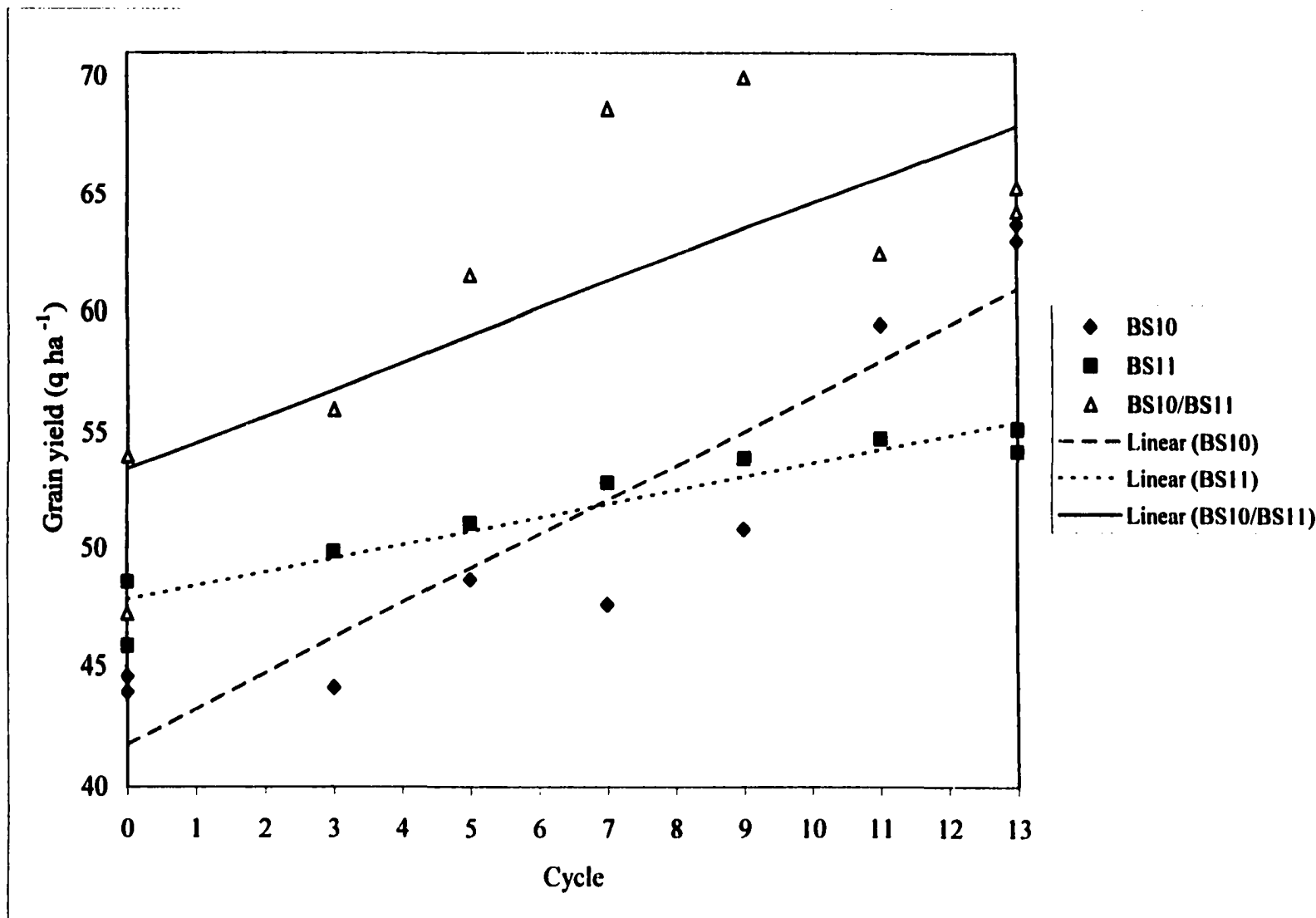


Figure 7. Grain yield trends of noninbred maize population means combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

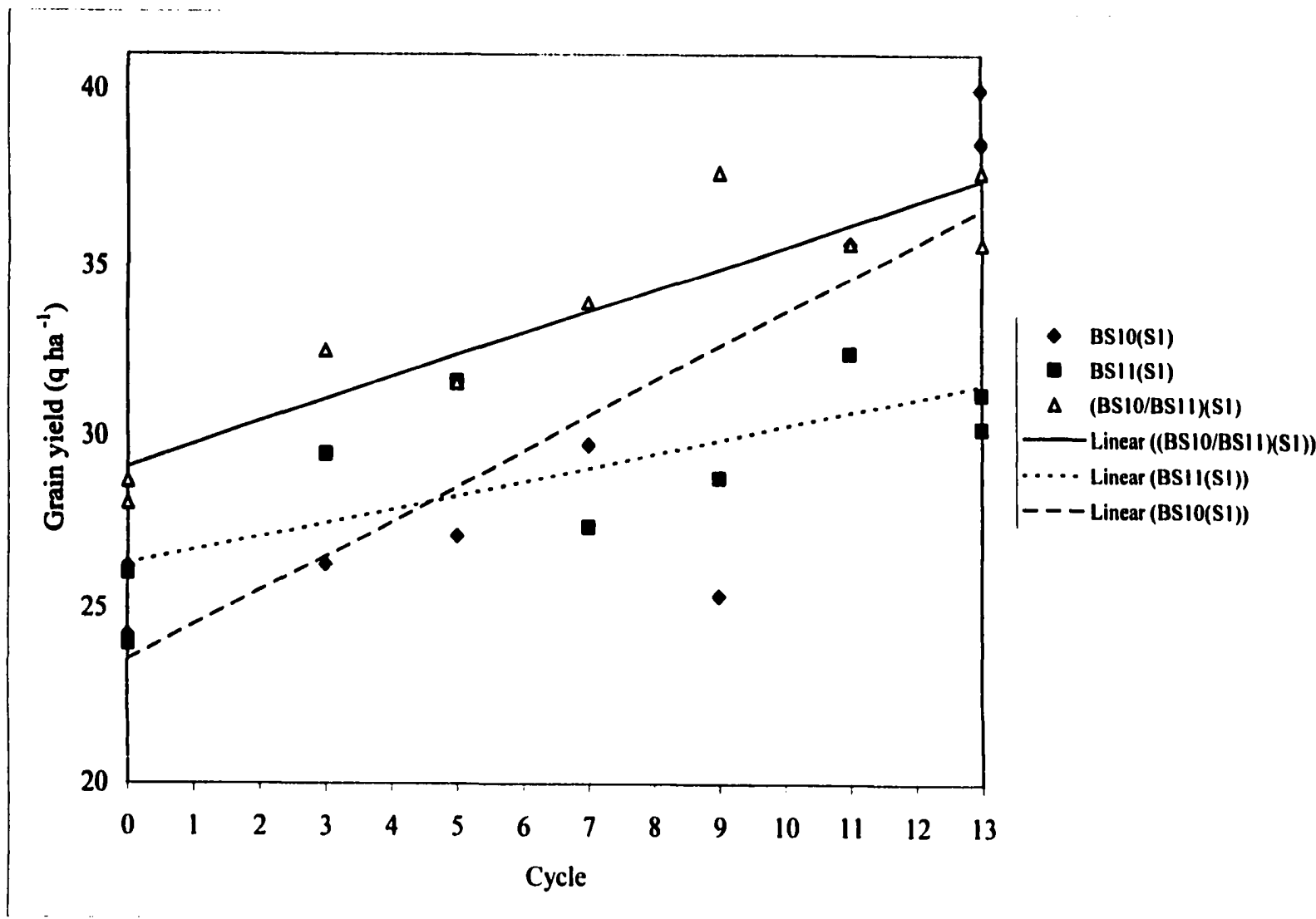


Figure 8. Grain yield trends of inbred maize population means combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

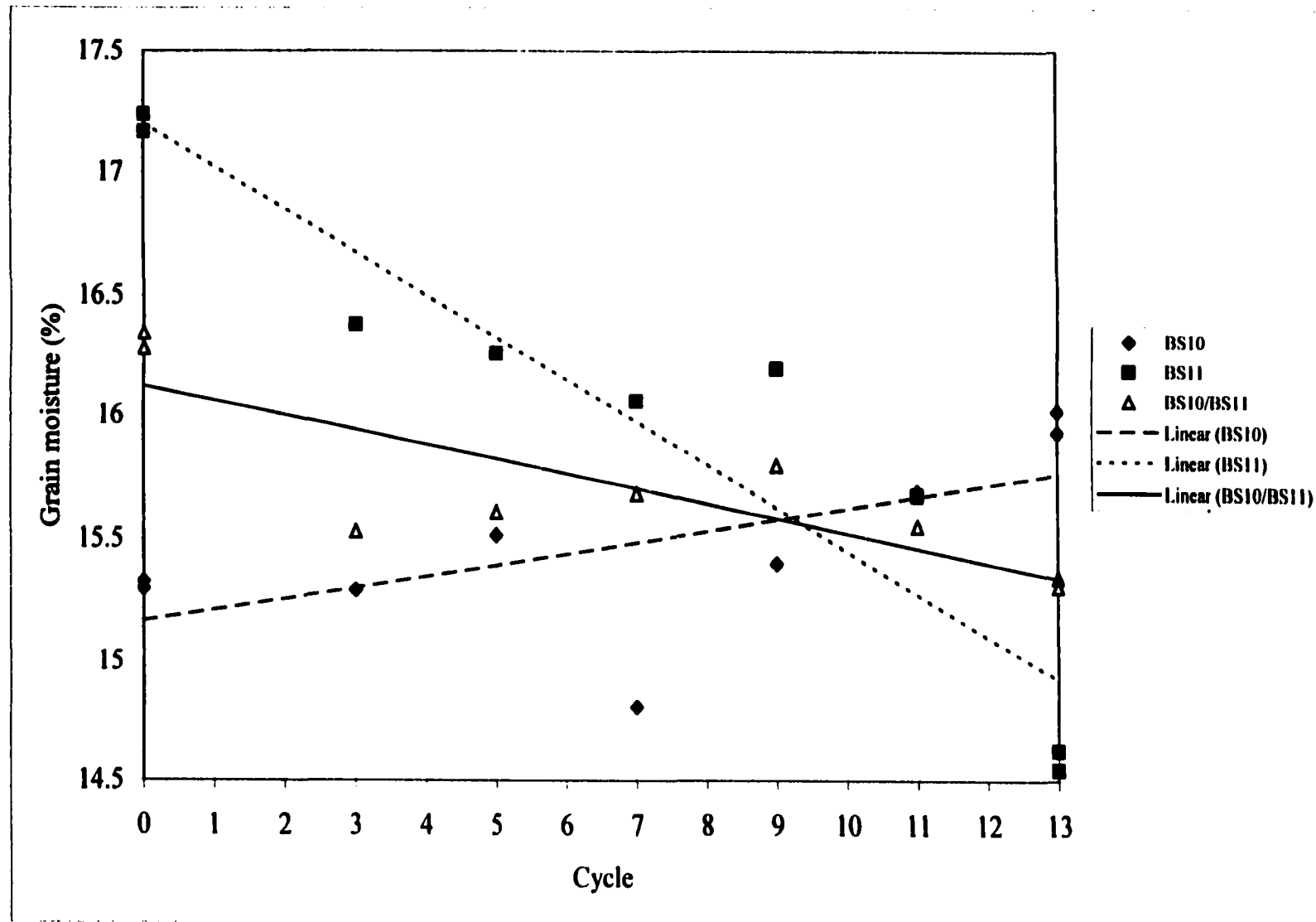


Figure 9. Grain moisture trends of noninbred maize population means combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

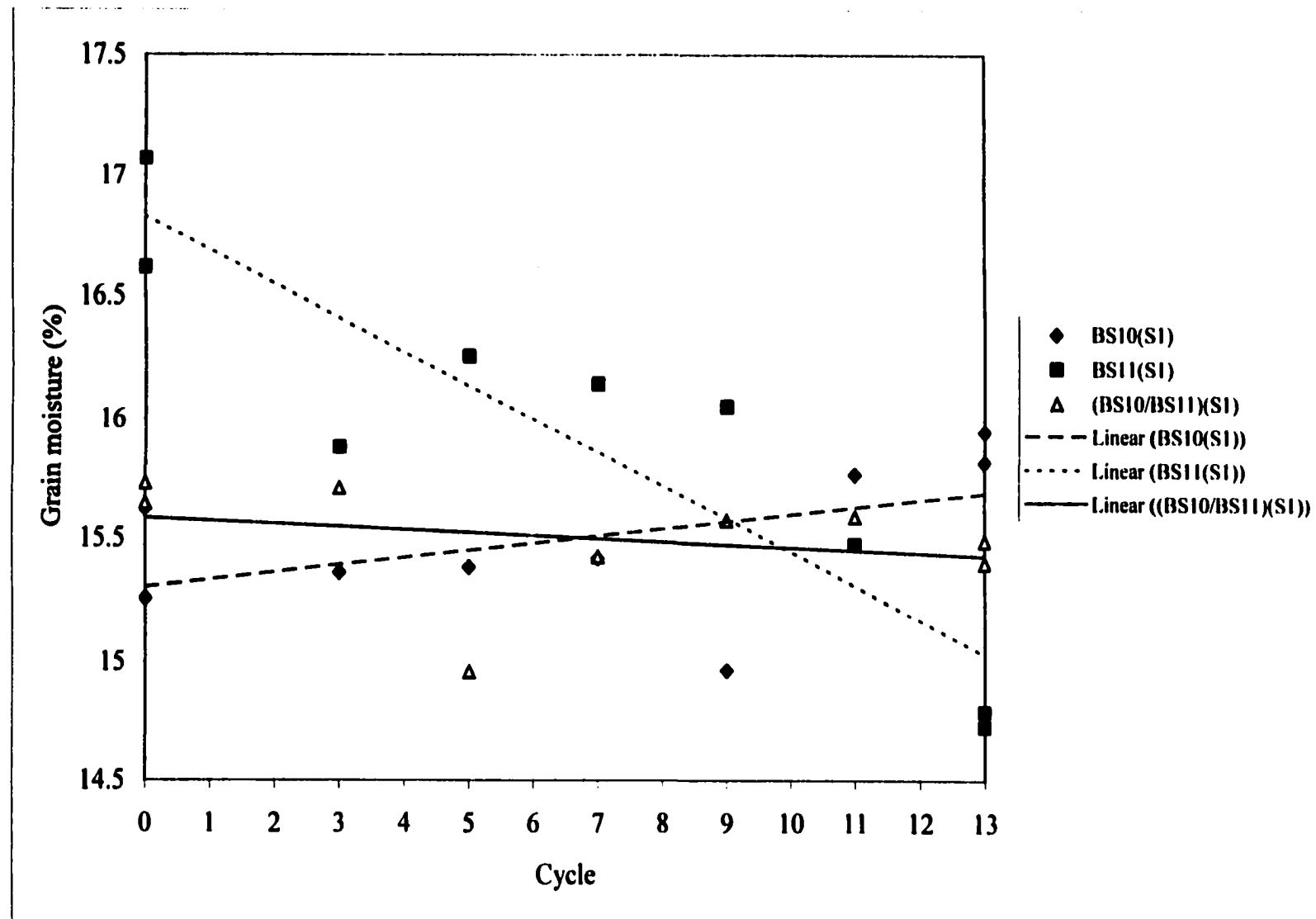


Figure 10. Grain moisture trends of inbred maize population means combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

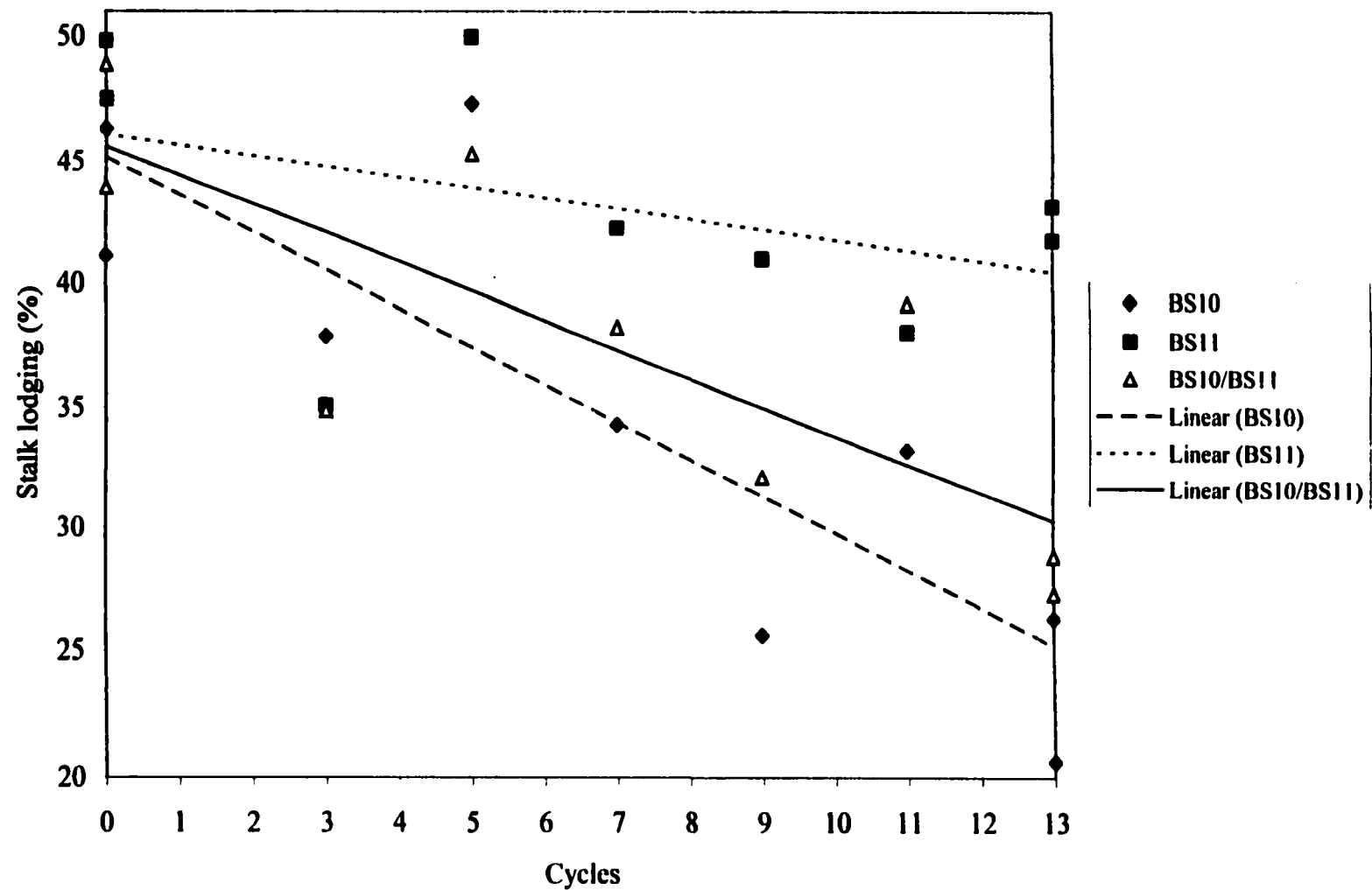


Figure 11. Stalk lodging trends of noninbred maize population means combined across six environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

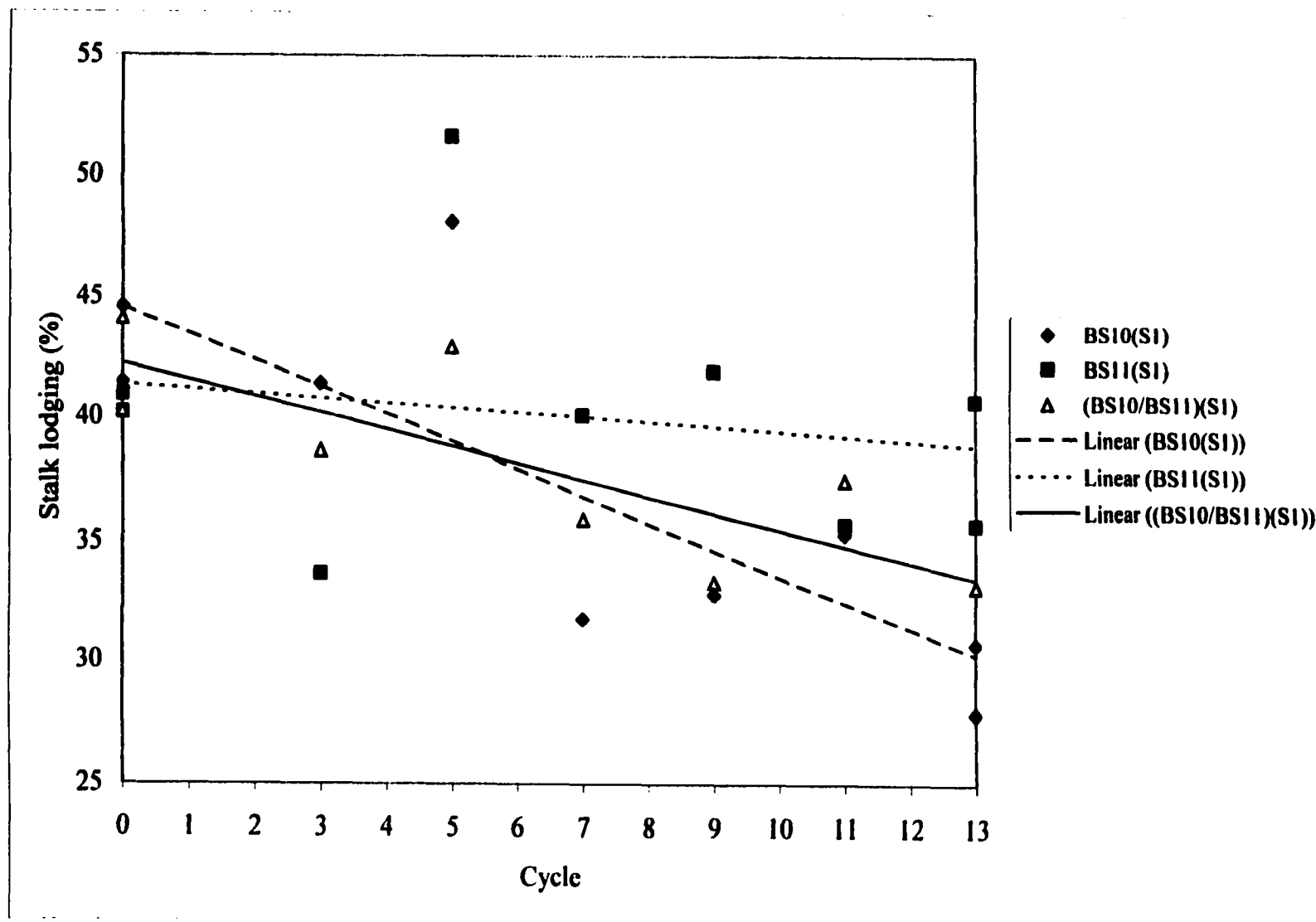


Figure 12. Stalk lodging trends of inbred maize population means combined across six environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

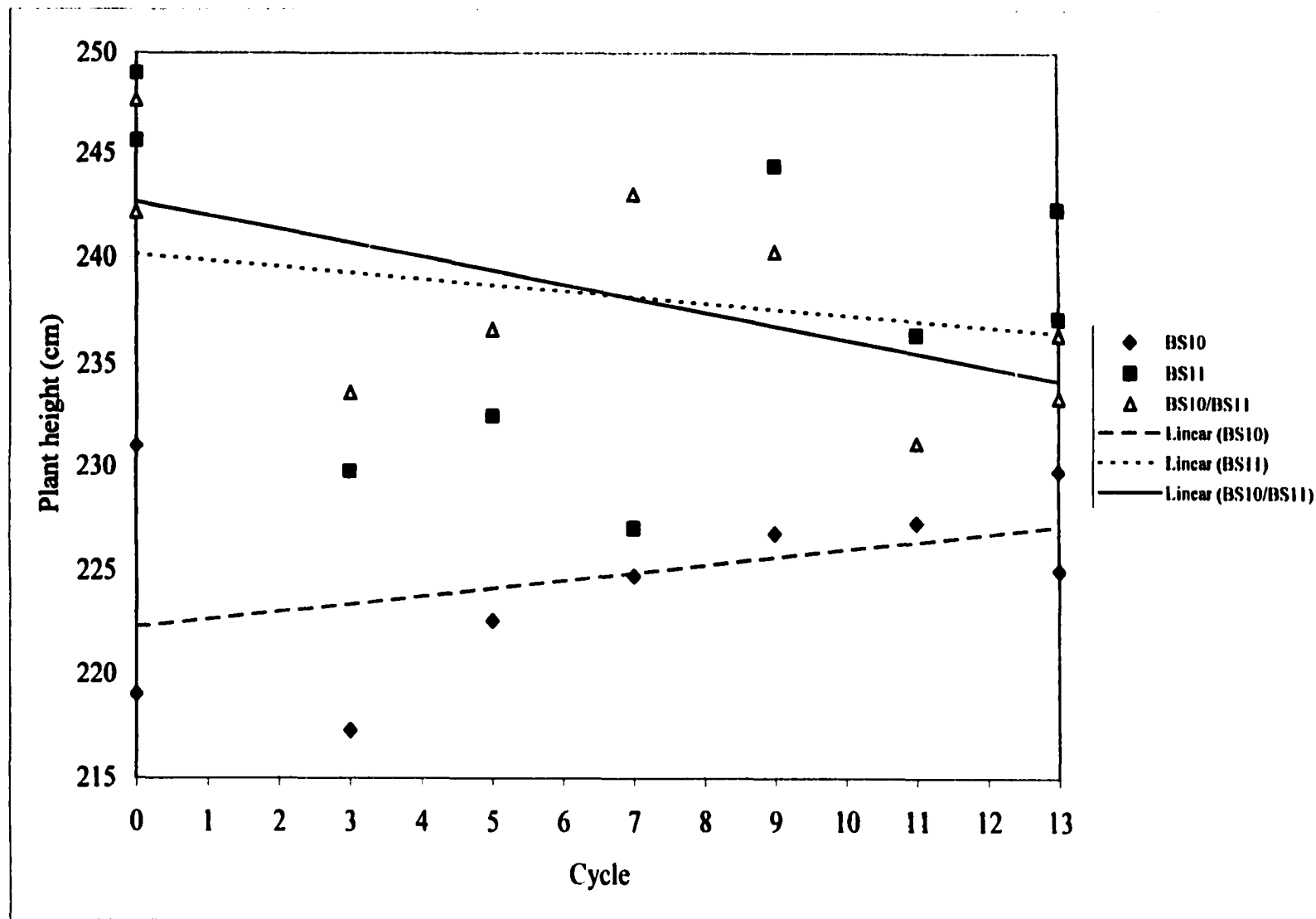


Figure 13. Plant height trends of noninbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

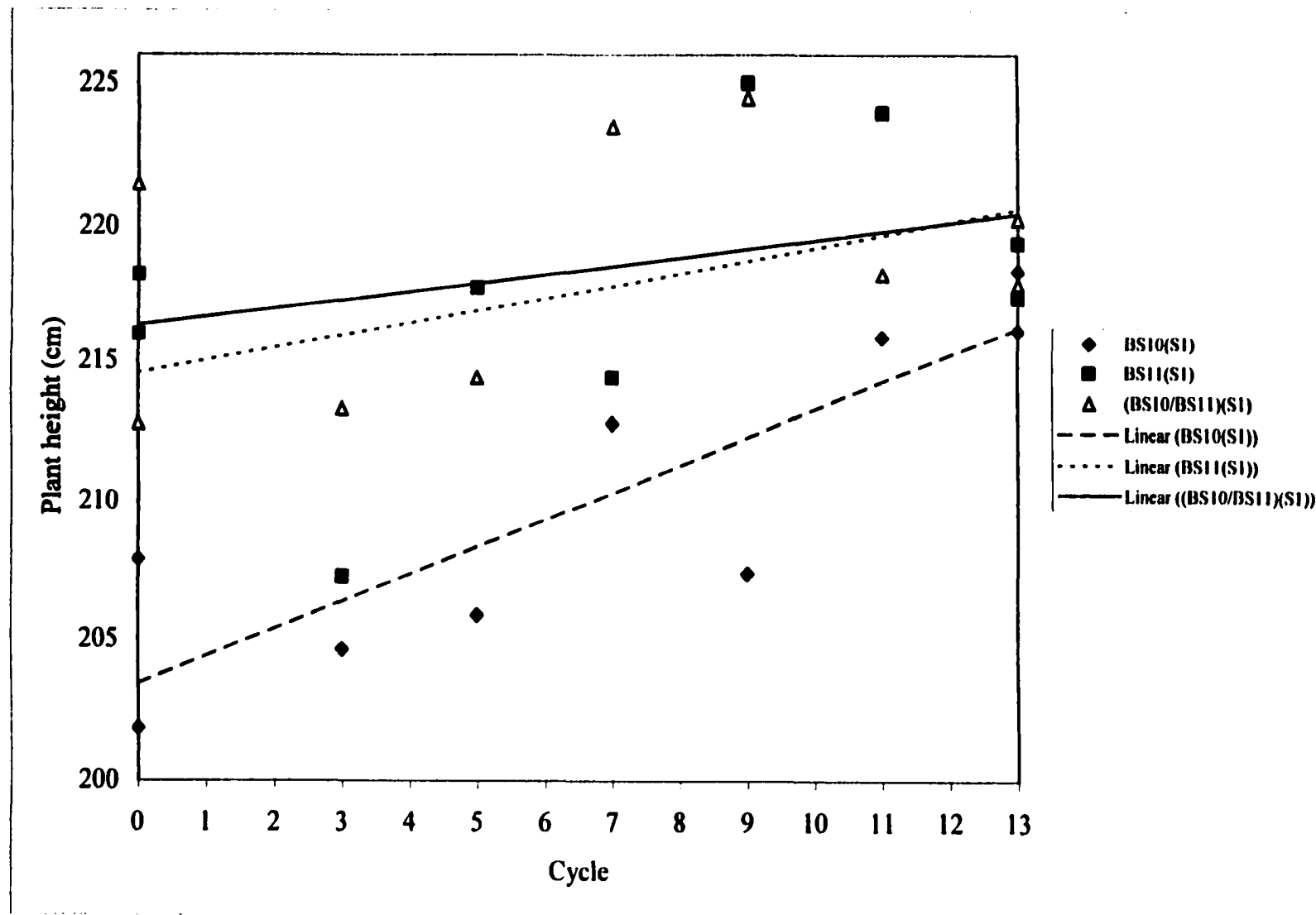


Figure 14. Plant height trends of inbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

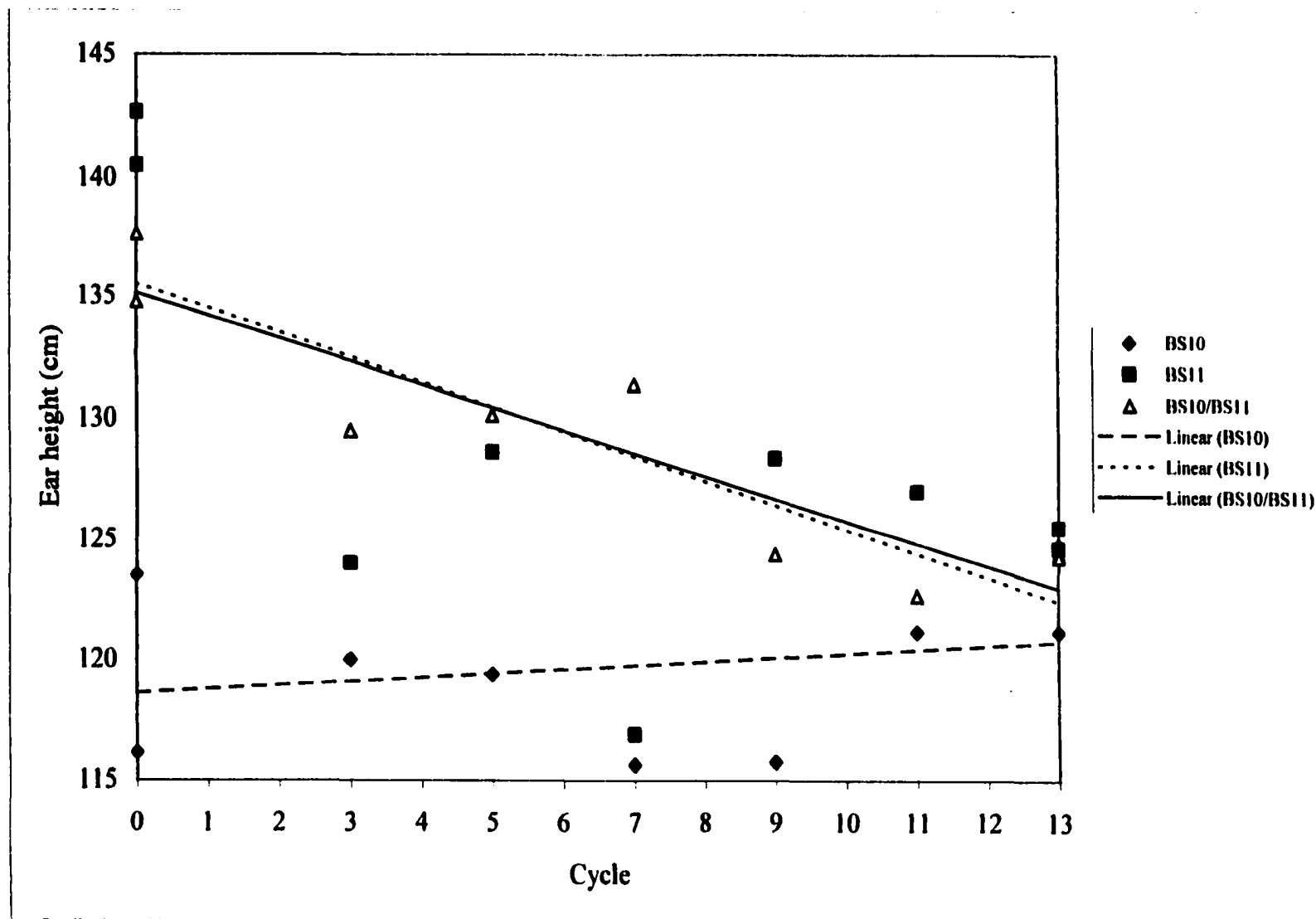


Figure 15. Ear height trends of noninbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

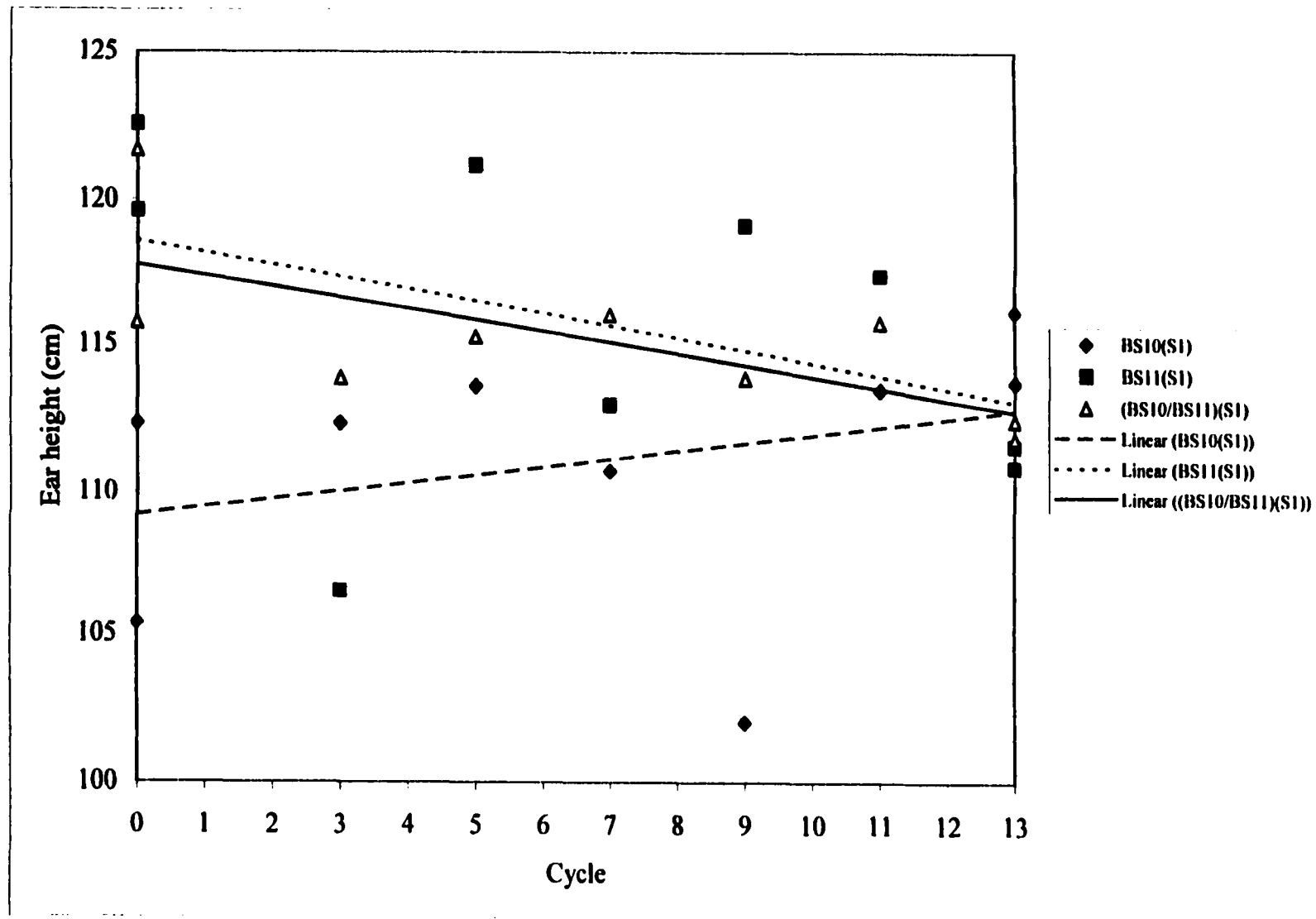


Figure 16. Ear height trends of inbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

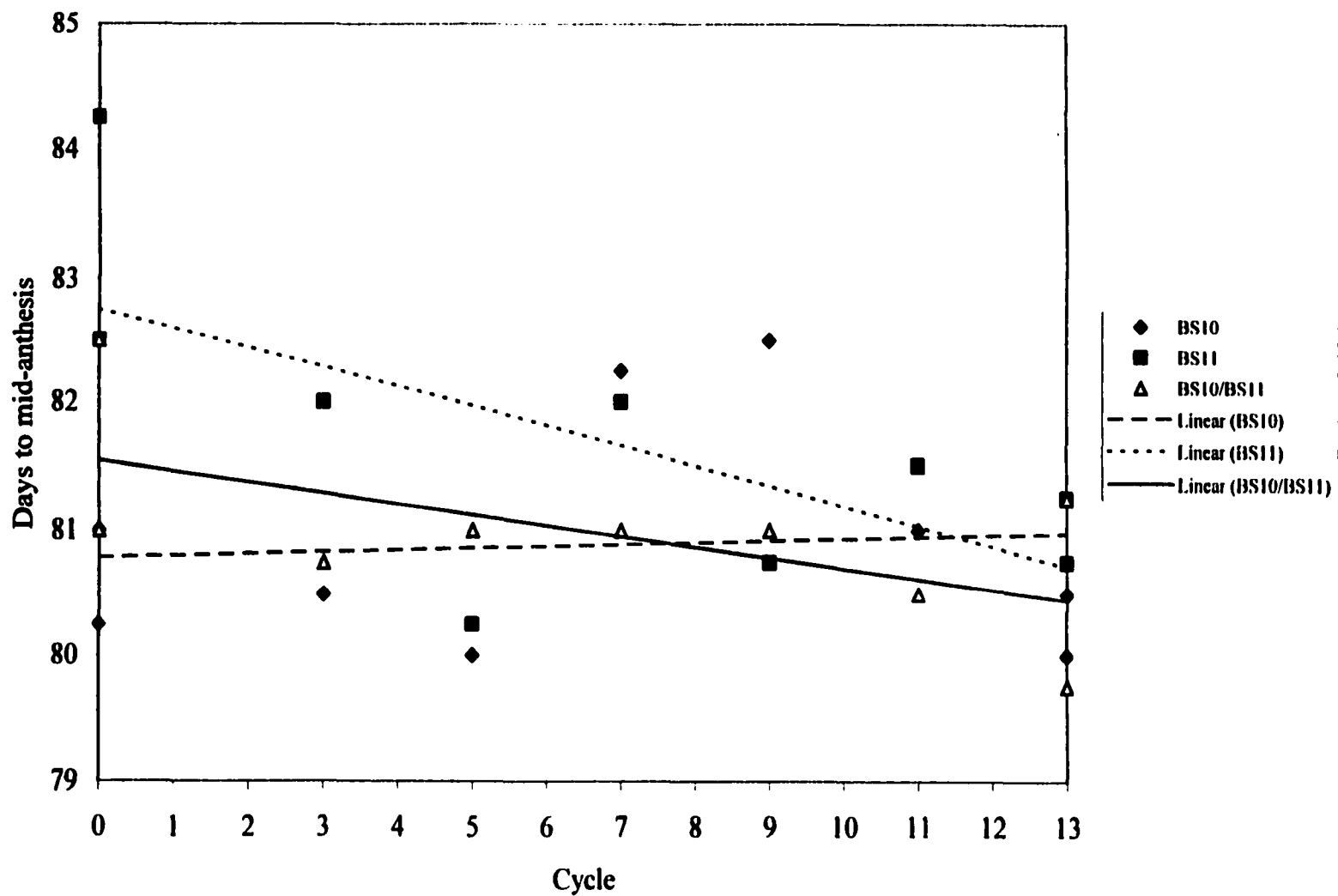


Figure 17. Days to mid-anthesis trends of noninbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

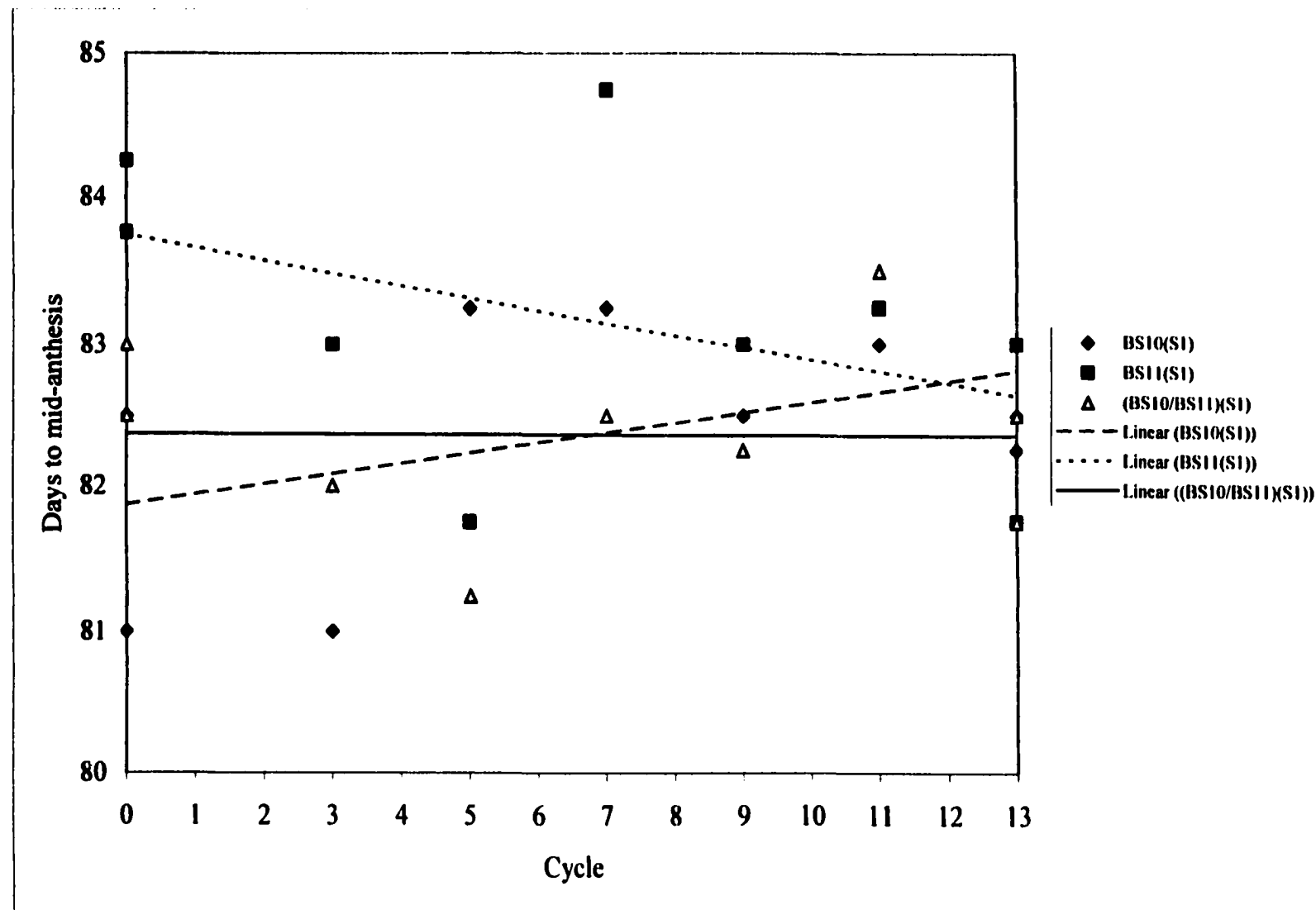


Figure 18. Days to mid-anthesis trends of inbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

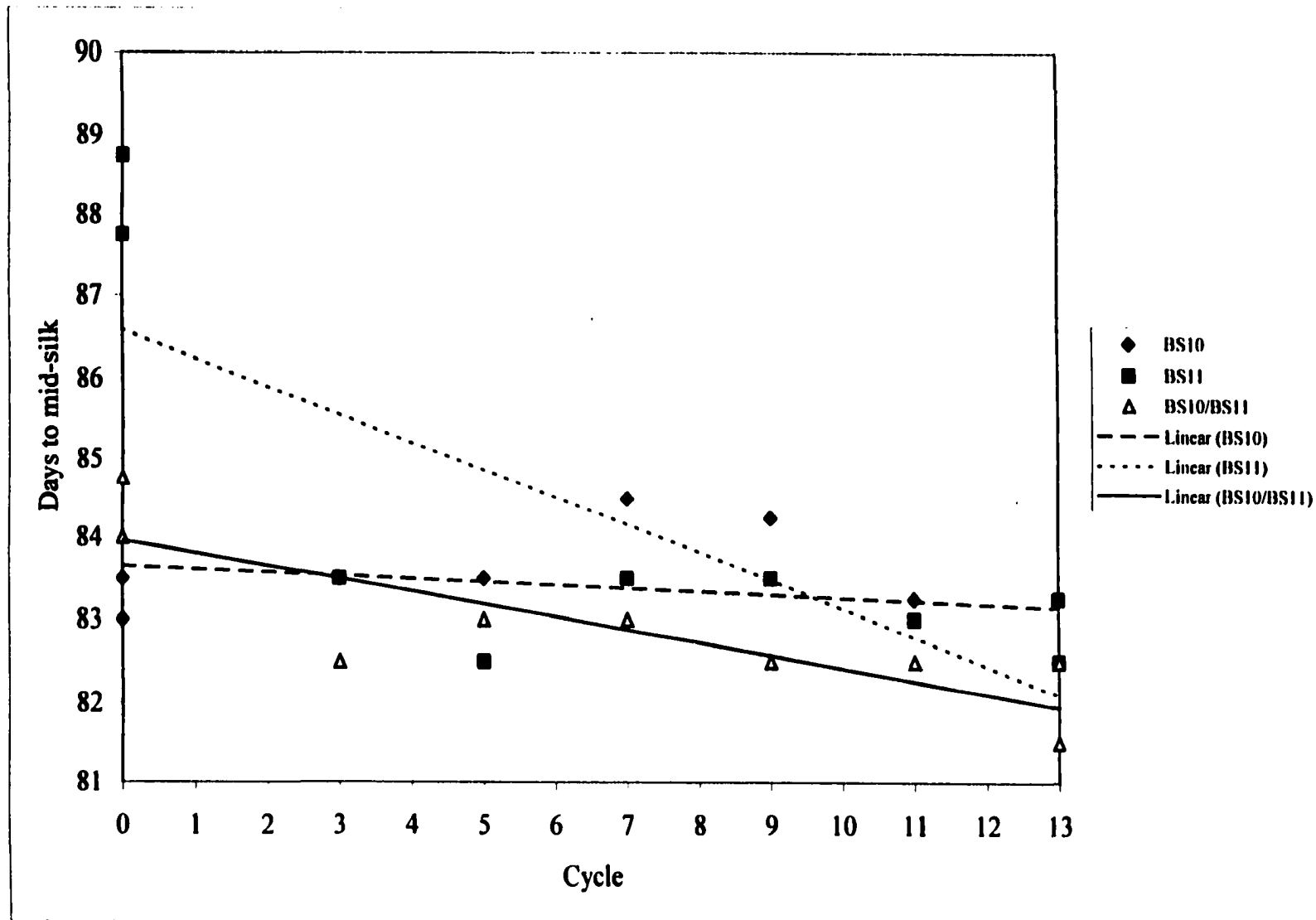


Figure 19. Days to mid-silk trends of noninbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

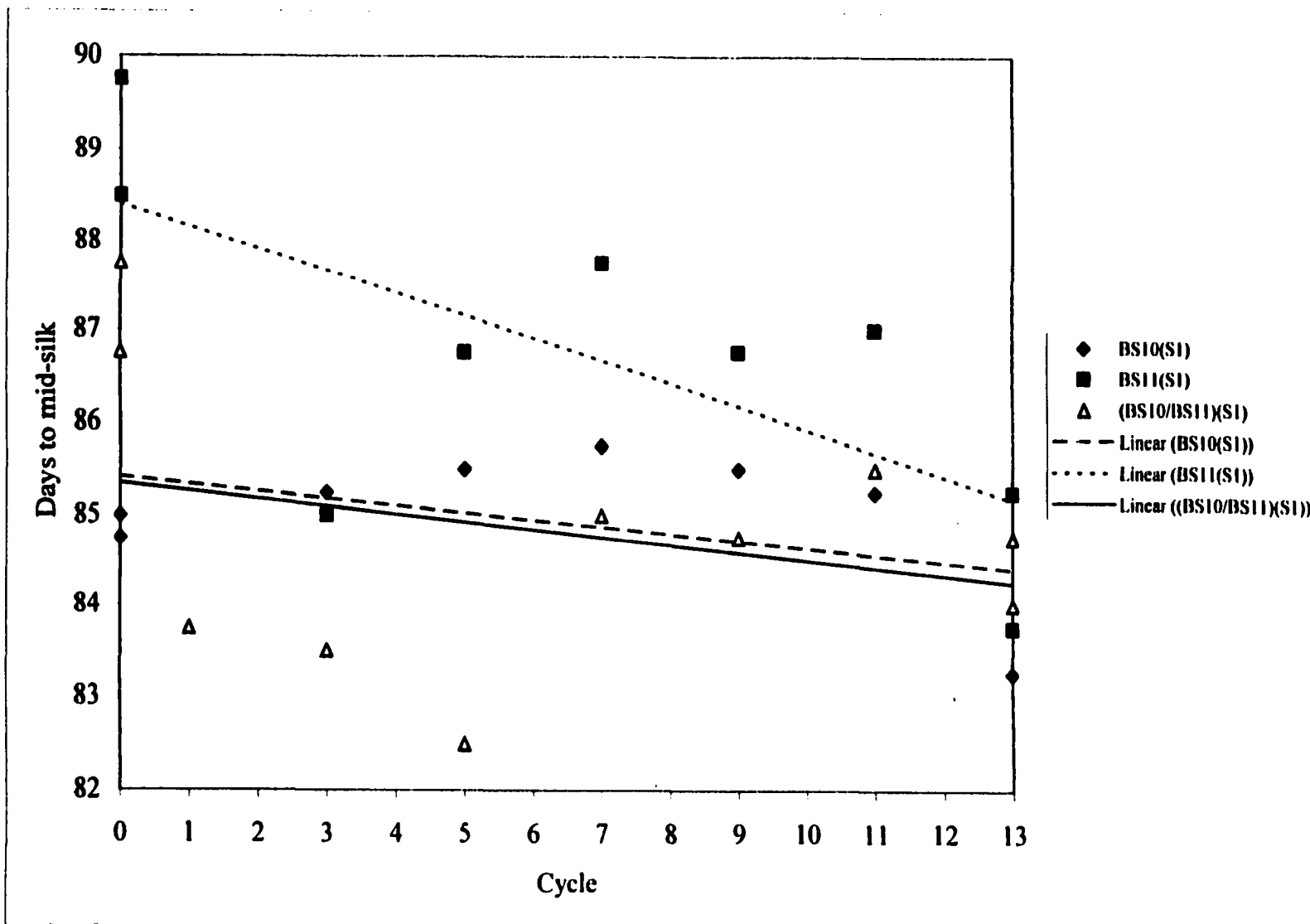


Figure 20. Days to mid-silk trends of inbred maize population means combined across four environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

(Tables 9 and 12). All improvement, however, occurs in the first nine cycles of selection, followed by a non-significant decrease from C9 to C11.

Other changes in means of selected traits include a non-linear decrease in grain moisture and a linear decrease in stalk lodging percentage. Grain moisture percentages show a decrease from 16.3 in C0 to 15.3 in C13 noninbred populations, with nearly all of the improvement occurring from C0 to C3. Improvement for grain moisture in the inbred population is not significant. Stalk lodging means have changed from 42.1 percent for the C0 noninbred population cross to 33.2 percent in the C13 population, a linear decrease of 2.6 percent per cycle. A correlated linear change of -1.6 percent per cycle is evident for the inbred population cross.

Among non-selected traits, only ear height in BS10/BS11, which has decreased at a rate of 0.7 percent, or 0.9 cm, per cycle, shows a linear response for either the inbred or noninbred population cross. Differences among entries within the noninbred population cross for plant height are significant, but no clear trends are evident over cycles, while no significant differences are present in the inbred population cross for either plant or ear height. Differences among entries for days to mid-anthesis within inbred and noninbred population crosses are not significant, although both show trends toward fewer days from planting to mid-anthesis. Significant decreases are evident at both levels of inbreeding for days to mid-silk.

Indirect changes associated with selection

Significant improvements based on LSD (0.05) values in BS10 and BS11, the indirect units of selection, have been made during 13 cycles of selection for grain yield

and stalk lodging in BS10, and grain yield, grain moisture, plant and ear height, and days to mid-anthesis and mid-silk in BS11 (Tables 8 and 10). Corresponding changes occurred for most traits in BS10(S₁) and BS11(S₁) (Tables 9 and 11). Response per cycle as a percentage of the C0 population mean and as a linear response per cycle, where appropriate as determined by the significance ($\text{probF} < 0.05$) of linear, quadratic, and deviation mean squares (Tables 4 through 7), are presented in Table 12. Regression coefficients significant at $\text{probF} < 0.05$ are presented along with R^2 values (Table 13). Cycle-to-cycle trends are shown in Figures 1 through 6. Best-fit linear trends, regardless of the linearity of the data, are shown in Figures 7 through 20.

Of all traits measured in BS10 and BS10(S₁), only stalk lodging for BS10 shows a linear improvement. Grain yield for BS10 increases at a non-linear rate of 3.3 percent per cycle, with the majority of the increase evident from C9 to C13. BS10(S₁) exhibits a similar trend and a response rate of 4.3 percent per cycle. Increasing trends for grain moisture are present for both inbred and noninbred populations, while stalk lodging decreases at a linear rate of 3.4 and a non-linear rate of 2.5 percent per cycle for BS10 and BS10(S₁), respectively. No significant differences exist among entries within BS10 noninbred populations for plant and ear height, or for BS10 noninbred and inbred populations for days to mid-anthesis and mid-silk. Plant height shows a linear increase of 0.5 percent per cycle for BS10(S₁), while ear height increases 6.1 cm from the C0 to the C13 population.

Improvements for traits in BS11 and BS11(S₁) are non-linear, with the exception of grain yield in the noninbred populations, at a rate of 1.2 percent per cycle. Significant

non-linear improvements include -1.2, -0.2, -0.9, -0.2 and -0.5 percent per cycle changes for grain moisture, plant and ear height, and days to mid-anthesis and mid-silk in BS11, and 1.8, -1.0, -0.6, and -0.4 percent per cycle changes for grain yield, grain moisture, ear height, and days to mid-silk in BS11(S₁), respectively. Non-significant improvements for stalk lodging from C0 to C13 are present for both the inbred and noninbred populations.

Heterosis and inbreeding depression

FR has been successful in improving heterosis between BS10 and BS11 for grain yield and stalk lodging over the first nine cycles of selection, though undesirable changes are evident from C9 to C11 (Table 14). Mid-parent heterosis for grain yield increases from 10.6 percent in C0 to 33.5 percent in C9, followed by a decrease to 9.3 percent in C11. A similar pattern is evident for high-parent heterosis, increasing from 7.2 percent in C0 to 29.8 in C9 and decreasing to 5.0 percent in C11. High-parent heterosis for stalk lodging changes from -4.6 percent in C0 to -21.6 percent in C9, followed by an increase to 2.9 percent in C11 and subsequent decrease to -34.0 percent in C13. Mid-parent heterosis for stalk lodging follows a similar, but more erratic, pattern.

Heterosis estimates for other traits follow either undesirable or erratic trends. High-parent heterosis for grain moisture changes from -5.2 percent in C0 to -2.5 percent in C9, followed by an increase to -0.9 percent in C11 and subsequent decrease to -4.1 percent in C13. Mid-parent grain moisture heterosis and heterosis for all non-selected traits suggest no consistent trends.

Inbreeding depression for grain yield generally increases from C0 to C7 for BS10/BS11 populations, while highest in C9 for BS10 and C7 for BS11, followed in all

Table 14. Mid-parent heterosis (HMP) and high-parent heterosis (HHP) in actual units and as a percentage for seven maize traits.

Trait	Cycle	HMP Units	HMP %	HHP Units	HHP %
Grain yield (q ha⁻¹)					
	0	4.86	10.62	3.40	7.19
	3	8.99	19.13	6.12	12.28
	5	11.63	23.31	10.40	20.36
	7	18.45	36.76	15.82	29.95
	9	17.56	33.54	16.04	29.76
	11	5.34	9.34	2.98	5.01
	13	5.77	9.78	1.44	2.28
Grain moisture (%)					
	0	0.05	0.33	-0.89	-5.17
	3	-0.31	-1.94	-0.85	-5.19
	5	-0.28	-1.75	-0.65	-4.00
	7	0.25	1.60	-0.38	-2.36
	9	0.00	-0.02	-0.40	-2.47
	11	-0.13	-0.82	-0.14	-0.87
	13	0.05	0.32	-0.65	-4.05
Stalk lodging (%)					
	0	0.22	0.48	-2.24	-4.60
	3	-1.64	-4.49	-3.06	-8.05
	5	-3.32	-6.83	-4.63	-9.26
	7	0.02	0.04	-3.94	-9.34
	9	-1.18	-3.54	-8.87	-21.64
	11	3.54	9.92	1.11	2.92
	13	-4.92	-14.94	-14.40	-33.95
Plant height (cm)					
	0	8.72	3.69	-2.44	-0.99
	3	10.13	4.53	3.88	1.69
	5	9.06	3.98	4.13	1.77
	7	17.13	7.58	16.00	7.05
	9	4.69	1.99	-4.13	-1.69
	11	-0.69	-0.30	-5.25	-2.22
	13	1.34	0.58	-4.81	-2.01
Ear height (cm)					
	0	5.50	4.21	-5.38	-3.80
	3	7.50	6.15	5.50	4.44
	5	6.13	4.94	1.50	1.17
	7	15.13	13.01	14.50	12.41
	9	2.31	1.89	-4.00	-3.12
	11	-1.44	-1.16	-4.38	-3.44
	13	0.31	0.25	-0.75	-0.60

Table 14. (continued)

Trait	Cycle	HMP Units	HMP %	HHP Units	HHP %
Days to mid-anthesis					
	0	-0.25	-0.30	-1.63	-1.95
	3	-0.50	-0.62	-1.25	-1.52
	5	0.88	1.09	0.75	0.93
	7	-1.13	-1.37	-1.25	-1.52
	9	-0.63	-0.77	-1.50	-1.82
	11	-0.75	-0.92	-1.00	-1.23
	13	-0.13	-0.16	-0.50	-0.62
Days to mid-silk					
	0	-1.38	-1.60	-3.88	-4.39
	3	-1.00	-1.20	-1.00	-1.20
	5	0.00	0.00	-0.50	-0.60
	7	-1.00	-1.19	-1.50	-1.78
	9	-1.38	-1.64	-1.75	-2.08
	11	-0.63	-0.75	-0.75	-0.90
	13	-0.69	-0.83	-0.88	-1.06

cases by decreases in the subsequent cycle (Table 15). Levels increase from 43.8 percent to 50.6 percent from C0 to C7 in BS10/BS11, followed by decreases to 46.1 percent in C9 and 42.9 percent in C11. By comparison, inbreeding depression from the check B73/MO17 to its F_2 equals 44.1 percent (Table 3). Trends are less obvious in BS10 and BS11, though both show large decreases from C9 to C11. For BS11 and the population cross, inbreeding depression increases from C11 to C13.

Response through cycle nine

In general, linear fit to the data is stronger for most selected traits through the first nine cycles of selection than from C0 to C13 (Tables 16, 17, 18, and 19). Significant linear grain yield mean squares for BS10, BS11, BS10/BS11 and (BS10/BS11)(S_1) and non-significant quadratic and deviation mean squares (Table 16) suggest linear models that explain 81.6, 91.1, 92.0, and 90.5 percent of the variation, respectively (Table 20). Linear models also fit the response through C9 for grain moisture in BS11, stalk lodging in BS10, BS10/BS11, BS10(S_1), and (BS10/BS11)(S_1), and plant height and days to mid-silk in (BS10/BS11)(S_1). Linear and non-linear responses for each trait are shown in Table 21, with regression coefficients and R^2 estimates shown when appropriate (Table 20). Linear trends, regardless of linear fit of the data, are shown in Figures 21 through 26.

Improvements have been made for all selected traits in all noninbred and inbred populations with the exceptions of grain moisture for BS10 and stalk lodging for BS11(S_1). Grain yield improves at a linear rate of 1.6 and 1.6 percent per cycle for the BS10 and BS11 noninbred populations, and 4.6 percent per cycle for the population

Table 15. Inbreeding depression for grain yield, calculated as the difference between noninbred and their corresponding inbred maize populations.

Noninbred population	Inbreeding depression (q ha ⁻¹)	Inbreeding depression %
BS10C0	19.03	42.99
BS10(FR)C3	17.84	40.42
BS10(FR)C5	21.49	44.17
BS10(FR)C7	17.83	37.48
BS10(FR)C9	25.48	50.11
BS10(FR)C11	23.81	40.04
BS10(FR)C13	24.09	38.04
BS11C0	22.20	47.04
BS11(FR)C3	20.37	40.85
BS11(FR)C5	19.54	38.23
BS11(FR)C7	25.42	48.11
BS11(FR)C9	25.08	46.53
BS11(FR)C11	22.38	40.87
BS11(FR)C13	23.97	43.85
BS10C0/BS11C0	22.18	43.84
BS10(FR)C3/BS11(FR)C3	23.54	42.04
BS10(FR)C5/BS11(FR)C5	29.98	48.75
BS10(FR)C7/BS11(FR)C7	34.77	50.64
BS10(FR)C9/BS11(FR)C9	32.25	46.12
BS10(FR)C11/BS11(FR)C11	26.79	42.90
BS10(FR)C13/BS11(FR)C13	28.12	43.41

Table 16. Analyses of variance through cycle nine for grain yield and grain moisture combined across seven environments for maize populations.

Source	Grain yield (q ha ⁻¹)		Grain Moisture (%)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment	6	2,352.2 **	6	84.7 **
Replications (Environment)	7	66.4	7	2.7
Entries	35	2,452.2 **	35	5.0 **
BS10	[4]	140.4	[4]	1.0 **
Linear	{1}	460.8 *	{1}	0.2
Quadratic	{1}	14.8	{1}	0.0
Deviations	{2}	43.0	{2}	1.9
BS11	[4]	138.2	[4]	4.7 **
Linear	{1}	550.0 *	{1}	15.2 **
Quadratic	{1}	1.9	{1}	3.3 *
Deviations	{2}	0.5	{2}	0.1
BS10/BS11	[4]	1,288.0 **	[4]	2.2 **
Linear	{1}	5,040.4 **	{1}	4.0
Quadratic	{1}	0.1	{1}	4.1 **
Deviations	{2}	55.7	{2}	0.3
BS10(S _i)	[4]	54.2	[4]	0.6
Linear	{1}	46.6	{1}	1.2
Quadratic	{1}	63.8	{1}	0.5
Deviations	{2}	53.3	{2}	0.3
BS11(S _i)	[4]	118.8 *	[4]	3.0 **
Linear	{1}	166.9	{1}	6.7 **
Quadratic	{1}	192.1 *	{1}	2.5 *
Deviations	{2}	58.1	{2}	1.4
(BS10/BS11)(S _i)	[4]	217.1 **	[4]	1.5
Linear	{1}	788.1 **	{1}	0.9
Quadratic	{1}	10.6	{1}	1.6
Deviations	{2}	34.9	{2}	1.7
Within duplicates	[6]	73.4	[6]	0.4
Among populations	[5]	15,512.2 **	[5]	24.1 **

Table 16. (continued)

Source	Grain yield (q ha ⁻¹)		Grain Moisture (%)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	210	59.9	210	0.5 **
BS10 by environment	[24]	77.6	[24]	0.2
Linear by environment	{6}	48.8	{6}	0.1
Quadratic by environment	{6}	89.8	{6}	0.2
Deviations by environment	{12}	85.8	{12}	0.2
BS11 by environment	[24]	71.2	[24]	0.5
Linear by environment	{6}	78.7	{6}	0.7
Quadratic by environment	{6}	60.9	{6}	0.5
Deviations by environment	{12}	72.6	{12}	0.3
BS10/BS11 by environment	[24]	46.0	[24]	0.4
Linear by environment	{6}	74.6	{6}	1.0 *
Quadratic by environment	{6}	62.1	{6}	0.2
Deviations by environment	{12}	23.6	{12}	0.2
BS10(S ₁) by environment	[24]	31.2	[24]	0.6
Linear by environment	{6}	13.2	{6}	0.9 *
Quadratic by environment	{6}	31.4	{6}	0.6
Deviations by environment	{12}	40.1	{12}	0.5
BS11(S ₁) by environment	[24]	31.1	[24]	0.4
Linear by environment	{6}	52.4	{6}	0.1
Quadratic by environment	{6}	15.8	{6}	0.3
Deviations by environment	{12}	28.1	{12}	0.6
(BS10/BS11)(S ₁) by environment	[24]	24.8	[24]	0.8 **
Linear by environment	{6}	28.5	{6}	1.5 **
Quadratic by environment	{6}	39.9	{6}	0.5
Deviations by environment	{12}	15.3	{12}	0.5
Within duplicates by environment	[36]	55.7	[36]	0.4
Among populations by environment	[30]	126.8 **	[30]	0.9 **
Pooled error	240†	56.4	235†	0.4
Total	498†		493†	

†Degrees of freedom adjusted for missing values

Table 17. Analyses of variance through cycle nine for root lodging and stalk lodging combined across six environments for maize populations.

Source	Root lodging (%)		Stalk lodging (%)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment	5	329.3 **	5	35,793.3 **
Replications (Environment)	6	32.9	6	165.9
Entries	35	8.9	35	443.8 **
BS10	[4]	2.4	[4]	950.4 **
Linear	{1}	1.0	{1}	2,119.2 **
Quadratic	{1}	1.4	{1}	736.3
Deviations	{2}	3.5	{2}	473.0
BS11	[4]	2.8	[4]	509.1 *
Linear	{1}	0.7	{1}	324.5
Quadratic	{1}	5.9	{1}	73.2
Deviations	{2}	2.3	{2}	819.4 *
BS10/BS11	[4]	7.7	[4]	600.4 *
Linear	{1}	1.8	{1}	1,290.9 **
Quadratic	{1}	23.3	{1}	6.8
Deviations	{2}	3.0	{2}	552.0
BS10(S ₁)	[4]	1.4	[4]	616.4 **
Linear	{1}	0.8	{1}	1,070.7 **
Quadratic	{1}	0.5	{1}	402.3
Deviations	{2}	2.1	{2}	496.3
BS11(S ₁)	[4]	8.6	[4]	500.6 *
Linear	{1}	0.5	{1}	95.4
Quadratic	{1}	0.6	{1}	28.1
Deviations	{2}	16.6	{2}	939.5 *
(BS10/BS11)(S ₁)	[4]	16.3	[4]	228.4 *
Linear	{1}	22.7	{1}	600.6 *
Quadratic	{1}	11.7	{1}	88.2
Deviations	{2}	15.5	{2}	112.5
Within duplicates	[6]	5.2	[6]	82.6
Among populations	[5]	25.0	[5]	282.9

Table 17. (continued)

Source	Root lodging (%)		Stalk lodging (%)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	175	8.2	175	155.7 **
BS10 by environment	[20]	3.5	[20]	189.5 *
Linear by environment	{5}	4.9	{5}	62.4
Quadratic by environment	{5}	2.3	{5}	179.4
Deviations by environment	{10}	3.4	{10}	258.2 **
BS11 by environment	[20]	4.6	[20]	121.5
Linear by environment	{5}	1.3	{5}	156.7
Quadratic by environment	{5}	5.2	{5}	112.0
Deviations by environment	{10}	5.9	{10}	108.7
BS10/BS11 by environment	[20]	8.8	[20]	191.5 *
Linear by environment	{5}	7.4	{5}	53.0
Quadratic by environment	{5}	15.5	{5}	106.1
Deviations by environment	{10}	6.1	{10}	303.5 **
BS10(S ₁) by environment	[20]	4.5	[20]	123.6
Linear by environment	{5}	9.6	{5}	54.3
Quadratic by environment	{5}	2.6	{5}	77.9
Deviations by environment	{10}	2.8	{10}	181.1
BS11(S ₁) by environment	[20]	10.8	[20]	170.4 *
Linear by environment	{5}	6.8	{5}	152.8
Quadratic by environment	{5}	4.9	{5}	193.0
Deviations by environment	{10}	15.7 *	{10}	168.0
(BS10/BS11)(S ₁) by environment	[20]	12.2	[20]	66.6
Linear by environment	{5}	11.0	{5}	38.0
Quadratic by environment	{5}	9.5	{5}	44.3
Deviations by environment	{10}	14.1	{10}	92.0
Within duplicates by environment	[30]	3.5	[30]	139.9
Among populations by environment	[25]	17.7 **	[25]	231.4 **
Pooled error	210	8.0	210	100.5
Total	431		431	

Table 18. Analyses of variance through cycle nine for plant height and ear height combined across four environments for maize populations.

Source	Plant height (cm)		Ear height (cm)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment	3	4,039.1 *	3	2,898.9 *
Replications (Environment)	4	542.9	4	295.6
Entries	35	1,422.5 **	35	728.2 **
BS10	[4]	112.9	[4]	44.4
Linear	{1}	21.0	{1}	132.0
Quadratic	{1}	280.8	{1}	17.8
Deviations	{2}	74.8	{2}	14.0
BS11	[4]	866.8 **	[4]	960.0 **
Linear	{1}	624.8 *	{1}	2,156.0 *
Quadratic	{1}	2,450.9 *	{1}	1,048.0 *
Deviations	{2}	195.7	{2}	318.1 *
BS10/BS11	[4]	213.7	[4]	200.7
Linear	{1}	78.0	{1}	624.8 *
Quadratic	{1}	417.9	{1}	1.0
Deviations	{2}	179.5	{2}	88.6
BS10(S ₁)	[4]	97.4	[4]	167.7
Linear	{1}	164.3	{1}	89.0
Quadratic	{1}	0.5	{1}	548.6 **
Deviations	{2}	112.4	{2}	16.6
BS11(S ₁)	[4]	329.3 **	[4]	361.6 **
Linear	{1}	203.8	{1}	43.6
Quadratic	{1}	689.5 **	{1}	402.7 **
Deviations	{2}	212.0 *	{2}	500.0 **
(BS10/BS11)(S ₁)	[4]	218.3	[4]	48.0
Linear	{1}	383.9 **	{1}	111.2
Quadratic	{1}	326.9	{1}	24.3
Deviations	{2}	81.2	{2}	28.3
Within duplicates	[6]	202.2	[6]	106.0
Among populations	[5]	8,244.3 **	[5]	3,544.1 **

Table 18. (continued)

Source	Plant height (cm)		Ear height (cm)	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	105	77.5	105	65.5
BS10 by environment	[12]	69.4	[12]	43.6
Linear by environment	{3}	148.3	{3}	64.9
Quadratic by environment	{3}	71.6	{3}	39.2
Deviations by environment	{6}	28.9	{6}	35.1
BS11 by environment	[12]	54.0	[12]	99.4 *
Linear by environment	{3}	45.2	{3}	183.2 *
Quadratic by environment	{3}	86.0	{3}	101.5
Deviations by environment	{6}	42.4	{6}	56.5
BS10/BS11 by environment	[12]	81.8	[12]	73.2
Linear by environment	{3}	92.0	{3}	42.2
Quadratic by environment	{3}	88.8	{3}	113.8
Deviations by environment	{6}	73.2	{6}	68.4
BS10(S ₁) by environment	[12]	74.4	[12]	53.5
Linear by environment	{3}	25.2	{3}	32.2
Quadratic by environment	{3}	6.7	{3}	15.0
Deviations by environment	{6}	132.9	{6}	83.3
BS11(S ₁) by environment	[12]	33.6	[12]	26.2
Linear by environment	{3}	71.9	{3}	37.6
Quadratic by environment	{3}	19.8	{3}	5.1
Deviations by environment	{6}	21.4	{6}	31.0
(BS10/BS11)(S ₁) by environment	[12]	91.2	[12]	64.3
Linear by environment	{3}	3.0	{3}	29.0
Quadratic by environment	{3}	75.8	{3}	44.9
Deviations by environment	{6}	143.0	{6}	91.7
Within duplicates by environment	[18]	130.1	[18]	100.5 *
Among populations by environment	[15]	63.2	[15]	49.4
Pooled error	140	95.2	140	51.2
Total	287		287	

Table 19. Analyses of variance through cycle nine for days to mid-anthesis and mid-silk combined across two environments for maize populations.

Source	Days to mid-anthesis		Days to mid-silk	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environment	1	1,272.1 *	1	1,521.0 *
Replications (Environment)	2	35.4	2	66.1
Entries	35	5.9 *	35	15.6 **
BS10	[4]	5.3	[4]	1.4
Linear	{1}	11.1	{1}	4.5
Quadratic	{1}	5.4	{1}	0.1
Deviations	{2}	2.4	{2}	0.6
BS11	[4]	8.4	[4]	34.1 **
Linear	{1}	21.2	{1}	89.5
Quadratic	{1}	3.8	{1}	42.5 *
Deviations	{2}	4.3	{2}	2.2
BS10/BS11	[4]	0.9	[4]	3.8
Linear	{1}	1.9	{1}	9.9
Quadratic	{1}	1.2 *	{1}	2.3
Deviations	{2}	0.3	{2}	1.5
BS10(S ₁)	[4]	4.1	[4]	0.6
Linear	{1}	6.5	{1}	0.9
Quadratic	{1}	0.2	{1}	0.3
Deviations	{2}	4.9	{2}	0.7
BS11(S ₁)	[4]	5.6	[4]	12.7
Linear	{1}	0.9	{1}	11.9
Quadratic	{1}	3.5	{1}	16.7
Deviations	{2}	9.0	{2}	11.1
(BS10/BS11)(S ₁)	[4]	1.6 *	[4]	18.7
Linear	{1}	0.9	{1}	24.1 *
Quadratic	{1}	3.1	{1}	39.6
Deviations	{2}	1.3	{2}	5.5
Within duplicates	[6]	2.9	[6]	1.5
Among populations	[5]	17.3	[5]	50.4 **

Table 19. (continued)

Source	Days to mid-anthesis		Days to mid-silk	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Entries by environments	35	2.8	35	2.2
BS10 by environment	[4]	2.9	[4]	3.9
Linear by environment	{1}	0.8	{1}	1.9
Quadratic by environment	{1}	10.2 *	{1}	10.8
Deviations by environment	{2}	0.3	{2}	1.5
BS11 by environment	[4]	3.4	[4]	1.1
Linear by environment	{1}	7.1 *	{1}	0.9
Quadratic by environment	{1}	1.4	{1}	0.2
Deviations by environment	{2}	2.6	{2}	1.6
BS10/BS11 by environment	[4]	1.2	[4]	0.8
Linear by environment	{1}	0.6	{1}	1.5
Quadratic by environment	{1}	0.0	{1}	0.1
Deviations by environment	{2}	2.0	{2}	0.8
BS10(S ₁) by environment	[4]	1.8	[4]	0.6
Linear by environment	{1}	2.9	{1}	0.9
Quadratic by environment	{1}	2.3	{1}	0.3
Deviations by environment	{2}	0.9	{2}	0.7
BS11(S ₁) by environment	[4]	3.6	[4]	2.7
Linear by environment	{1}	5.3	{1}	0.4
Quadratic by environment	{1}	2.2	{1}	5.8
Deviations by environment	{2}	3.5	{2}	2.2
(BS10/BS11)(S ₁) by environment	[4]	0.1	[4]	3.1
Linear by environment	{1}	0.1	{1}	0.0
Quadratic by environment	{1}	0.0	{1}	9.9
Deviations by environment	{2}	0.2	{2}	1.2
Within duplicates by environment	[6]	1.4	[6]	2.1
Among populations by environment	[5]	7.4 **	[5]	2.8
Pooled error	70	1.8	70	2.8
Total	143		143	

Table 20. Regression coefficients with standard errors, and R^2 parameters for selection response of six maize traits† to nine cycles of selection. Parameters for which mean squares are not significant are not shown.

Population	Parameter	Grain yield q ha ⁻¹	Grain moisture %	Stalk lodging %	Plant height cm	Ear height cm	Days to mid-silk
BS10	b ₀	43.837±0.863		45.219±3.933			
	b ₁	0.696±0.165		-1.612±0.752			
	b ₂						
	R ²	0.816		0.534			
BS11	b ₀	47.303±0.622	17.193±0.049		247.396±2.974	141.443±3.639	
	b ₁	0.760±0.119	-0.319±0.029		-8.035±1.775	-6.544±2.171	
	b ₂				0.884±0.203	0.545±0.249	
	R ²	0.911	0.989		0.876	0.830 ‡	
BS10/BS11	b ₀	50.336±1.770		45.600±3.246		135.580±1.628	
	b ₁	2.301±0.339		1.258±0.621		-1.072±0.311	
	b ₂						
	R ²	0.920		0.507		0.747	
BS10(S1)	b ₀			44.587±3.490			
	b ₁			-1.146±0.667			
	b ₂						
	R ²			0.424			
BS11(S1)	b ₀		16.792±0.221				
	b ₁		-0.251±0.132				
	b ₂		0.020±0.015				
	R ²		0.684				
(BS10/BS11)(S1)	b ₀	28.419±0.773		42.617±1.836	214.950±3.161		86.233±1.149
	b ₁	0.910±0.148		-0.858±0.351	0.840±0.605		-0.298±0.220
	b ₂						
	R ²	0.905		0.599	0.326		0.315

† No parameters for root lodging or days to mid-anthesis were significant. These traits are not shown.

‡ Deviation mean squares are significant.

Table 21. Response for eight maize traits to nine cycles of selection shown in actual units. Linear responses are shown where the linear mean squares are significant and the quadratic and deviations mean squares are not significant.

Trait	Population	Response (C0 to C9) (Units)	Response per cycle (C9-C0)/9 (Units)	Response per cycle Linear (Units)	Response per cycle CO to C9 (% of CO mean)	Response per cycle Linear (% of intercept)
Grain yield (q ha⁻¹)						
	BS10	6.573	0.730	0.696	1.650	1.588
	BS11	6.705	0.745	0.760	1.579	1.607
	BS10/BS11	19.347	2.150	2.301	4.250	4.571
	BS10(S1)	0.130	0.014		0.057	
	BS11(S1)	3.828	0.425		1.702	
	(BS10/BS11)(S1)	9.271	1.030	0.910	3.626	3.202
Grain moisture (%)						
	BS10	0.086	0.010		0.062	
	BS11	-1.007	-0.112	-0.319	-0.651	-1.855
	BS10/BS11	-0.518	-0.058		-0.353	
	BS10(S1)	-0.475	-0.053		-0.342	
	BS11(S1)	-0.793	-0.088		-0.523	
	(BS10/BS11)(S1)	-0.115	-0.013		-0.081	
Root lodging (%)						
	BS10	-0.344	-0.038		-3.180	
	BS11	-0.573	-0.064		-2.883	
	BS10/BS11	0.149	0.017		1.472	
	BS10(S1)	-0.443	-0.049		-3.399	
	BS11(S1)	0.957	0.106		4.096	
	(BS10/BS11)(S1)	0.455	0.051		3.990	
Stalk lodging (%)						
	BS10	-18.136	-2.015	-1.612	-4.608	
	BS11	-7.682	-0.854		-1.754	
	BS10/BS11	-14.310	-1.590	-1.258	-3.426	-2.759
	BS10(S1)	-10.181	-1.131	-1.146	-2.631	-2.570
	BS11(S1)	1.347	0.150		0.369	
	(BS10/BS11)(S1)	-8.794	-0.977	-0.858	-2.319	-2.013

Table 21. (continued)

Trait	Population	Response (C0 to C9) (Units)	Response per cycle (C9-C0)/9 (Units)	Response per cycle Linear (Units)	Response per cycle C0 to C9 (% of C0 mean)	Response per cycle Linear (% of intercept)
Plant height (cm)						
	BS10	1.750	0.194		0.086	
	BS11	-2.938	-0.326		-0.132	
	BS10/BS11	-4.625	-0.514		-0.210	
	BS10(S1)	2.500	0.278		0.136	
	BS11(S1)	7.875	0.875		0.403	
	(BS10/BS11)(S1)	7.375	0.819	0.840	0.377	0.391
Ear height (cm)						
	BS10	-4.063	-0.451		-0.377	
	BS11	-13.188	-1.465		-1.035	
	BS10/BS11	-11.813	-1.313	-1.072	-0.964	-0.791
	BS10(S1)	-6.875	-0.764		-0.702	
	BS11(S1)	-1.938	-0.215		-0.178	
	(BS10/BS11)(S1)	-4.813	-0.535		-0.451	
Days to mid-anthesis						
	BS10	1.875	0.208		0.258	
	BS11	-2.625	-0.292		-0.350	
	BS10/BS11	-0.750	-0.083		-0.102	
	BS10(S1)	0.750	0.083		0.102	
	BS11(S1)	-1.000	-0.111		-0.132	
	(BS10/BS11)(S1)	-0.500	-0.056		-0.067	
Days to mid-silk						
	BS10	1.000	0.111		0.133	
	BS11	-4.750	-0.528		-0.598	
	BS10/BS11	-1.875	-0.208		-0.247	
	BS10(S1)	0.625	0.069		0.082	
	BS11(S1)	-2.375	-0.264		-0.296	
	(BS10/BS11)(S1)	-2.500	-0.278	-0.298	-0.318	-0.346

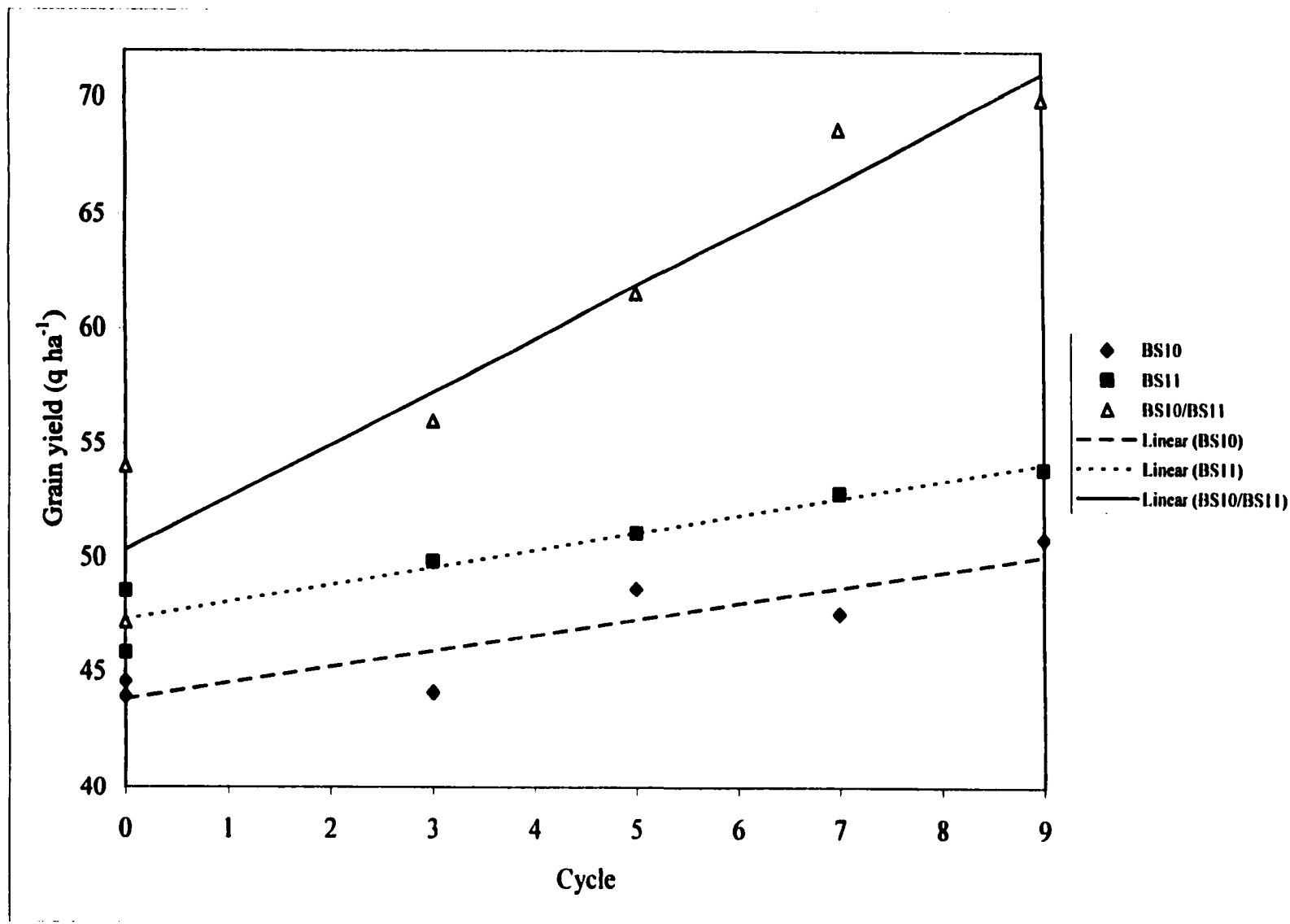


Figure 21. Grain yield trends of noninbred maize population means through cycle nine combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

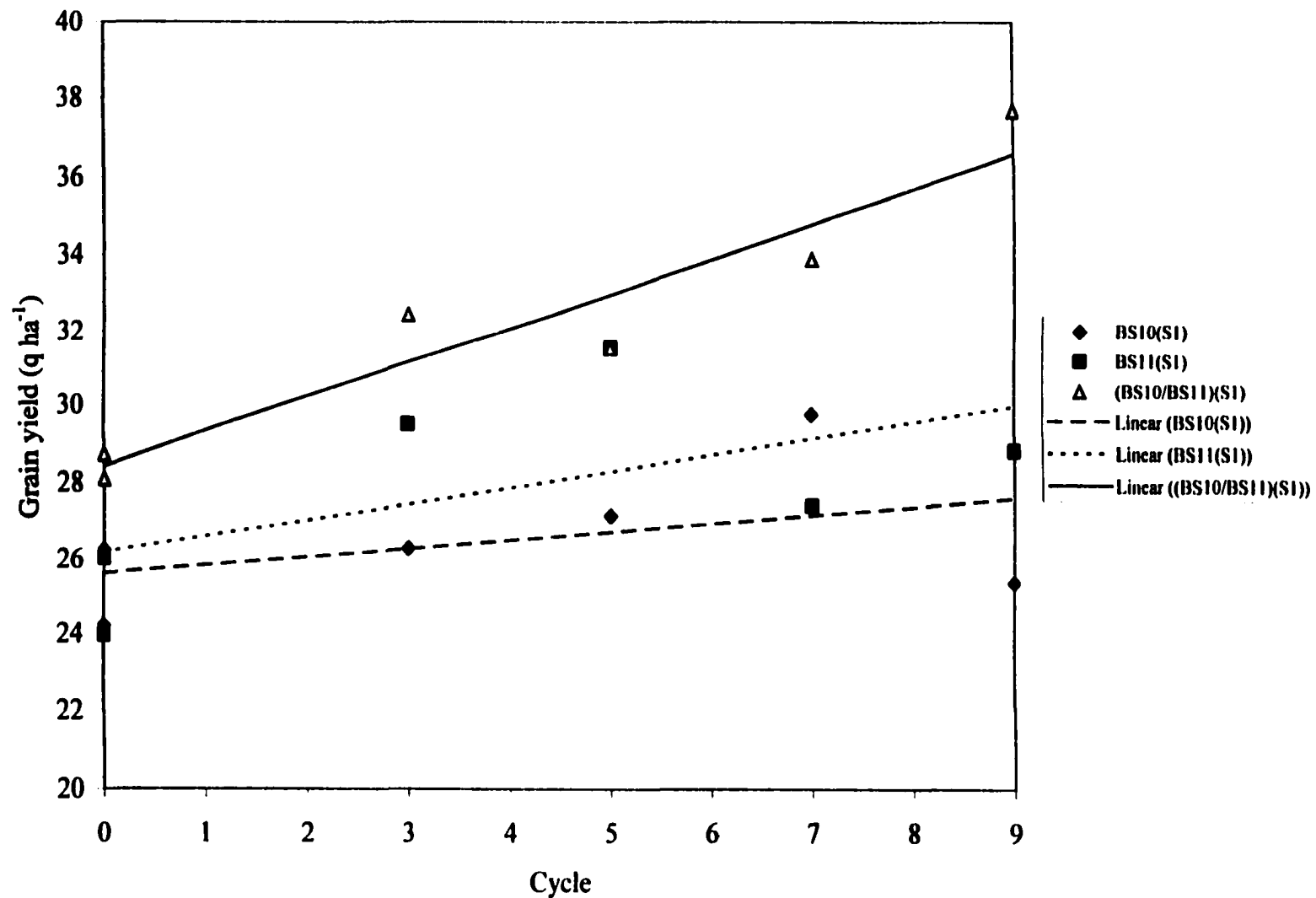


Figure 22. Grain yield trends of inbred maize population means through cycle nine combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

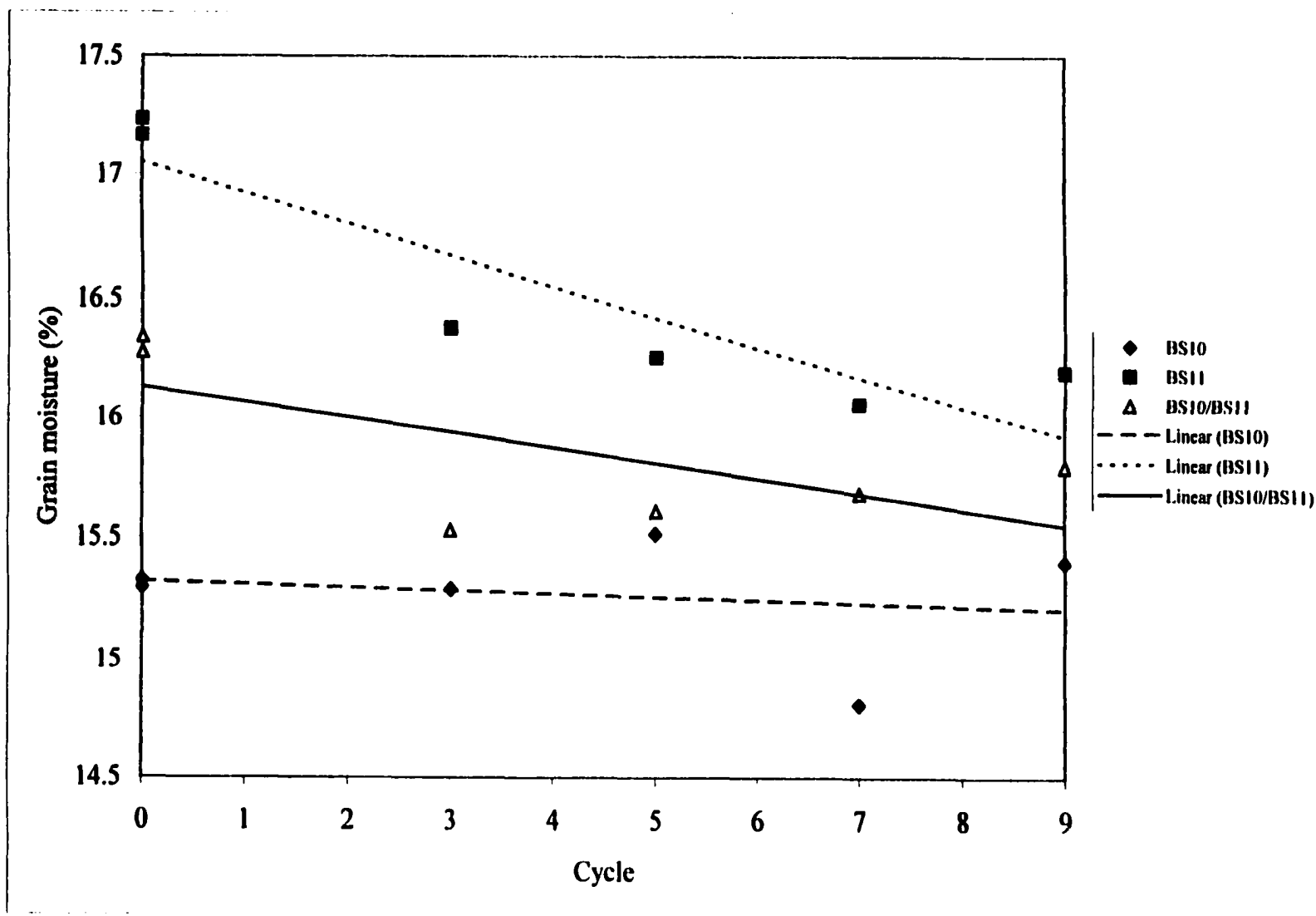


Figure 23. Grain moisture trends of noninbred maize population means through cycle nine combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

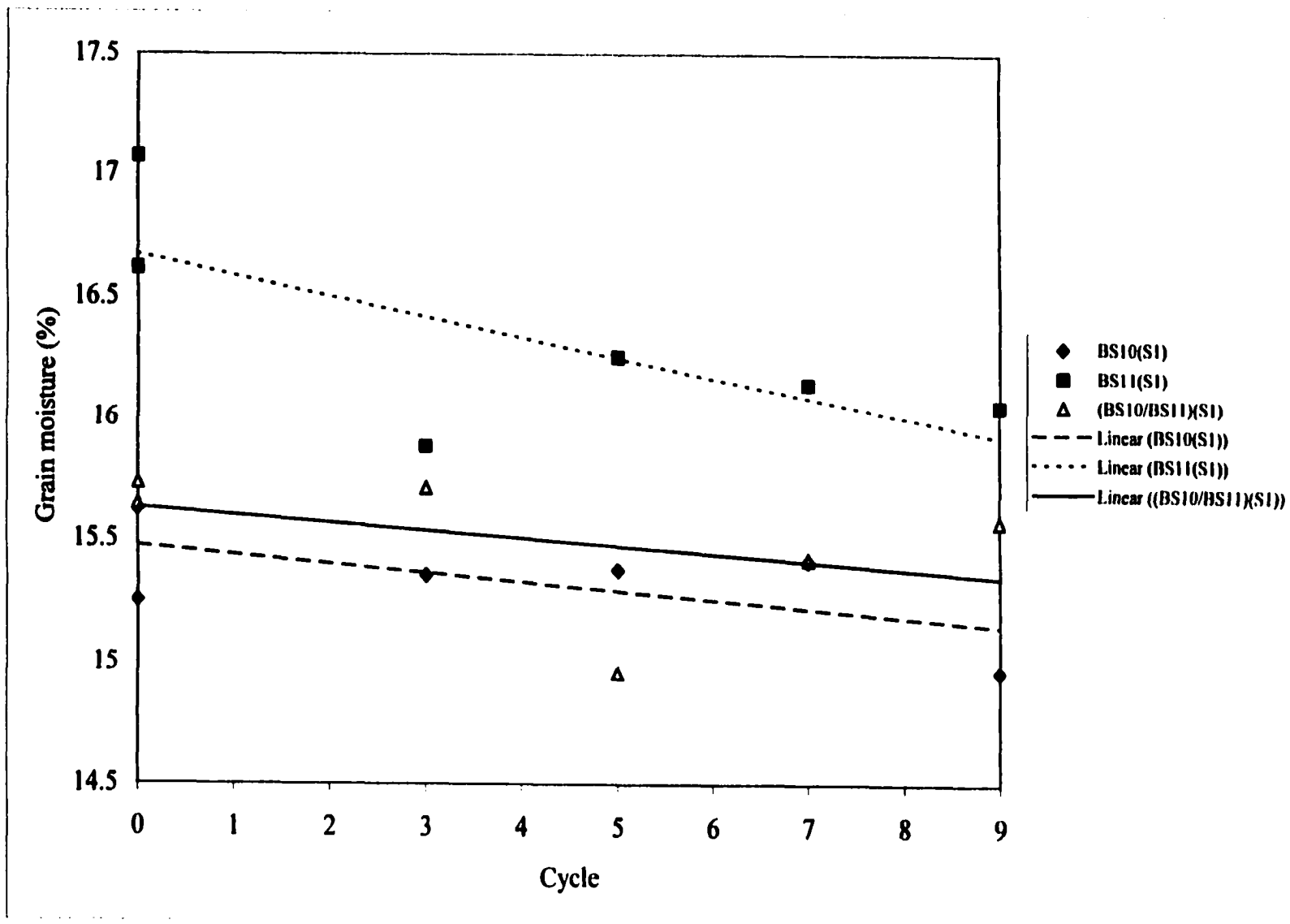


Figure 24. Grain moisture trends of inbred maize population means through cycle nine combined across seven environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

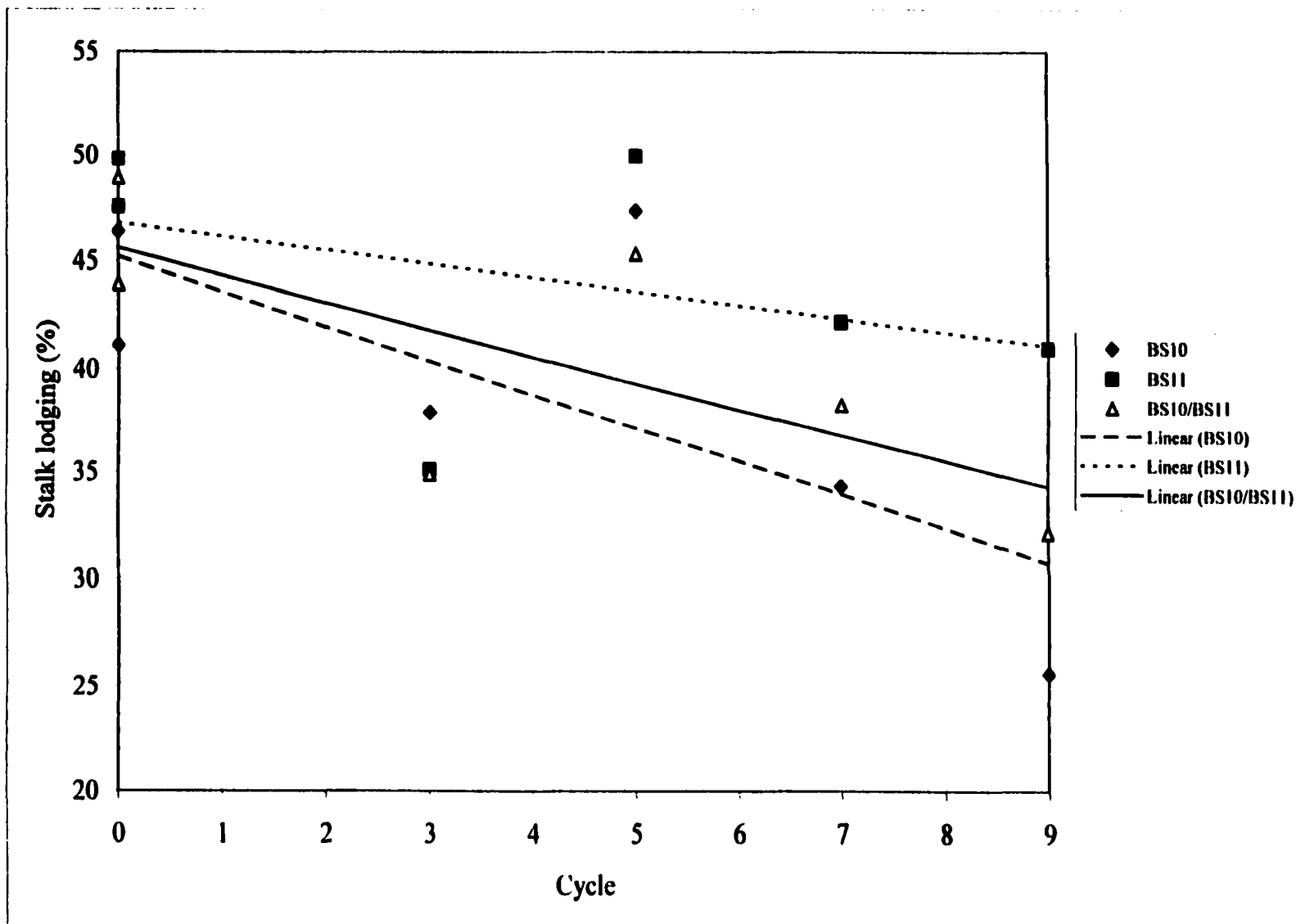


Figure 25. Stalk lodging trends of noninbred maize population means through cycle nine combined across six environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

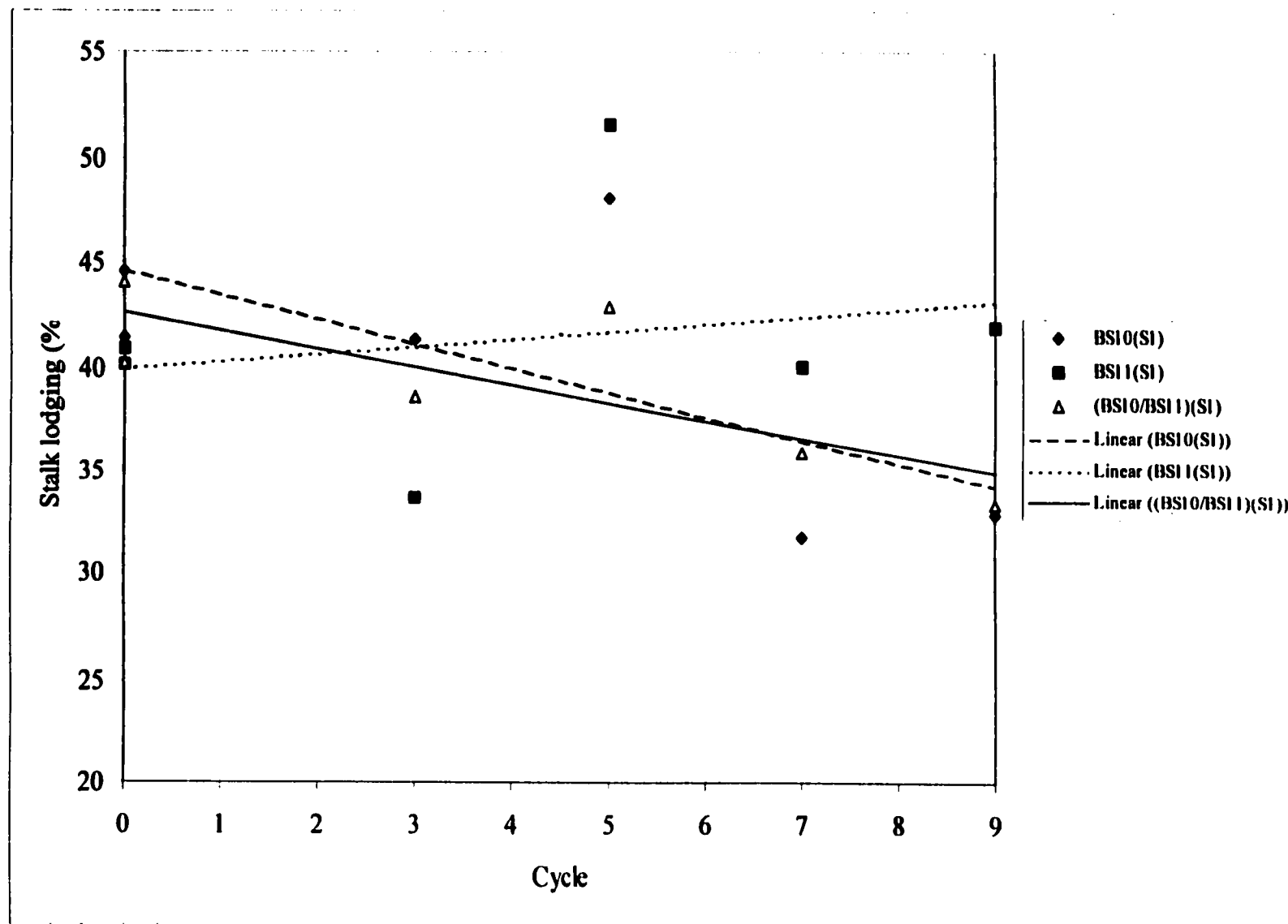


Figure 26. Stalk lodging trends of inbred maize population means through cycle nine combined across six environments. Best-fit lines for the population cross and BS10 and BS11 populations *per se* are shown, regardless of linearity of the data.

cross. Inbred population grain yield increases at non-linear rates of 0.1 and 1.7 percent per cycle for BS10 and BS11, and at a linear rate of 3.2 percent per cycle for the inbred population cross. Stalk lodging improvement is greatest in BS10, which shows a decrease at a non-linear rate of 4.6 percent per cycle. Non-linear improvement in BS11 equals 1.8 percent per cycle, while a linear decrease of 2.8 percent per cycle is evident for BS10/BS11.

Experiment two

As for experiment one, results indicate improvements in means of all selected traits from C0 to C13 for BS10(S₁) and BS11(S₁). Mean grain yields for 65 BS10C0 and BS10C13, 42 BS11C0, and 65 BS11C13 random S₁ lines equal 33.9, 45.5, 29.0, and 39.1 q ha⁻¹, respectively, combined across two replications each at Ames and Ankeny, Iowa (Table 22). Overall C0 population means for grain yield are higher at Ames, while C13 population performances are higher at Ankeny. Changes in other traits from C0 to C13 S₁ populations include 0.1, -0.1, -20.7, 12.6, 4.6, -0.3, and -1.3 in BS10 and -3.2, -0.8, -9.5, 4.0, -12.5, -2.7, and -3.9 in BS11 for grain moisture, root lodging, stalk lodging, plant and ear height, and days to mid-anthesis and mid-silk, respectively (Table 23). Entry means combined across environments are listed in Appendix B.

Analyses of variance

Differences among the four populations are highly significant for grain moisture, plant and ear height and days to mid-silk, significant for days to mid-anthesis, and nearly significant (probF = 0.0525) for grain yield and for stalk lodging (probF = 0.08) (Tables 24, 25, and 26). Populations by environment interaction mean squares are highly

Table 22. Means of 65† random S1 maize lines at Ames and Ankeny, Iowa, and combined across environments for grain yield (YLD), grain moisture (MST), root lodging (RL), stalk lodging (SL), plant height (PH), ear height (EH), and days mid-anthesis (DTA) and mid-silk DTS).

Environment	Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm	DTA	DTS
Ames	BS10C0	34.37	17.73	0.01	61.05	212.22	113.10	85.03	88.05
	BS10C13	42.12	17.68	0.05	32.28	223.36	117.62	84.21	85.91
	BS11C0	29.21	19.92	0.33	59.88	229.02	130.12	87.69	91.27
	BS11C13	35.37	16.30	0.05	46.34	229.38	116.09	84.77	87.34
Ankeny	BS10C0	33.43	15.33	1.02	21.07	194.78	103.19	79.04	81.19
	BS10C13	48.90	15.54	0.71	8.40	208.87	107.96	79.29	80.67
	BS11C0	28.76	17.25	3.08	20.17	208.30	116.23	81.62	85.12
	BS11C13	42.88	14.46	1.72	14.69	215.86	105.28	79.19	81.25
Combined	BS10C0	33.90	16.53	0.52	41.06	203.50	108.15	82.03	84.62
	BS10C13	45.51	16.61	0.38	20.34	216.12	112.79	81.75	83.29
	BS11C0	28.98	18.59	1.70	40.02	218.66	123.17	84.65	88.20
	BS11C13	39.12	15.38	0.89	30.52	222.62	110.68	81.98	84.29

†BS11C0 maize population means represent 42 random S1 lines.

Table 23. Indirect response to 13 cycles of FR in total units, units per cycle and percent per cycle for eight traits in the BS10(S1) and BS11(S1) maize populations.

Trait	Population	Response (Units)	Response per cycle (Units)	Response per cycle (% of C0)
Grain yield (q ha ⁻¹)	BS10(S1)	11.61	0.893	2.634
	BS11(S1)	10.14	0.780	2.692
Grain moisture (%)	BS10(S1)	0.08	0.006	0.037
	BS11(S1)	-3.21	-0.247	-1.328
Root lodging (%)	BS10(S1)	-0.14	-0.011	-2.071
	BS11(S1)	-0.81	-0.062	-3.665
Stalk lodging (%)	BS10(S1)	-20.72	-1.594	-3.882
	BS11(S1)	-9.50	-0.731	-1.826
Plant height (cm)	BS10(S1)	12.62	0.971	0.477
	BS11(S1)	3.96	0.305	0.139
Ear height (cm)	BS10(S1)	4.64	0.357	0.330
	BS11(S1)	-12.49	-0.961	-0.780
Days to mid-anthesis	BS10(S1)	-0.28	-0.022	-0.026
	BS11(S1)	-2.67	-0.205	-0.243
Days to mid-silk	BS10(S1)	-1.33	-0.102	-0.121
	BS11(S1)	-3.91	-0.301	-0.341

Table 24. Combined analysis of variance for two traits across two environments for S1 maize lines.

Source	Grain yield		Grain moisture	
	Degrees of freedom	Mean square	Degrees of freedom	Mean square
Environments	1	3040.5 *	1	2621.8 **
Replications(Environments)	2	47.3	2	3.1
Populations	3	10966.1	3	350.6 **
Populations*Environments	3	1,226.0 **	3	6.7 *
Error (a) [populations*replications(environments)]	6	49.4	6	1.1
Lines(populations)	233	291.2 **	233	7.1 **
Lines(BS10C0)	[64]	225.5 **	[64]	8.0 **
Lines(BS10C13)	[64]	339.1 **	[64]	4.7 **
Lines(BS11C0)	[41]	283.8 **	[41]	16.3 **
Lines(BS11C13)	[64]	313.7 **	[64]	2.9 **
Lines(Populations)*Environments	233	66.5 **	233	0.7 **
Lines(BS10C0)*environments	[64]	57.2 *	[64]	0.7 *
Lines(BS10C13)*environments	[64]	80.4 **	[64]	0.7 *
Lines(BS11C0)*environments	[41]	49.9	[41]	1.3 **
Lines(BS11C13)*environments	[64]	72.6 **	[64]	0.5
Error (b) (pooled)	457†	39.7	456†	0.5
Total	938†		937†	

† Degrees of freedom adjusted for missing values

Table 25. Combined analysis of variance for four traits across two environments for S1 maize lines.

Source	Degrees of freedom	Root lodging Mean square	Stalk lodging Mean square	Plant height Mean square	Ear height Mean square
Environments	1	469.7 **	261,741.7 **	719.7 **	27,619.9 *
Replications(Environments)	2	1.1	1,641.0	222.1	902.0
Populations	3	68.3	22,665.8	17,344.9 **	8,289.9 **
Populations*Environments	3	42.2 **	3,524.0	538.2	179.3
Error (a) [populations*replications(environments)]	6	3.7	2,330.6	522.4	307.0
Lines(populations)	233	17.3 **	1,093.0 **	833.4 **	533.0 **
Lines(BS10C0)	[64]	4.9	901.1 **	1,111.6 **	711.7 **
Lines(BS10C13)	[64]	2.8	861.2 **	568.5 **	348.2 **
Lines(BS11C0)	[41]	75.5 *	1,601.6 **	769.6 **	662.0 **
Lines(BS11C13)	[64]	7.0	1,190.9 **	861.1 **	456.6 **
Lines(Populations)*Environments	233	10.7 **	375.9 **	83.2	55.7
Lines(BS10C0)*environments	[64]	4.4 *	322.7 **	95.0	76.2 **
Lines(BS10C13)*environments	[64]	2.4	428.2 **	97.1	42.1
Lines(BS11C0)*environments	[41]	39.7 **	377.7 **	77.7	59.9
Lines(BS11C13)*environments	[64]	6.9 **	375.8 **	61.0	46.0
Error (b) (pooled)	466	2.9	114.2	85.8	47.9
Total	947				

Table 26. Combined analysis of variance for two traits across two environments for S1 maize lines.

Source	Degrees of freedom	Days to mid-anthesis	Days to mid-silk
		Mean square	Mean square
Environments	1	7424.5 **	8755.4 **
Replications(Environments)	2	1.7	2.8
Populations	3	348.1 *	869.2 **
Populations*Environments	3	16.6	28.4
Error (a) [populations*replications(environments)]	6	12.3	24.8
Lines(populations)	233	12.6 **	18.5 **
Lines(BS10C0)	[64]	12.4 **	25.7 **
Lines(BS10C13)	[64]	8.6 **	12.4 **
Lines(BS11C0)	[41]	20.3 **	25.7 **
Lines(BS11C13)	[64]	11.9 **	13.0 **
Lines(Populations)*Environments	233	1.9 *	3.3 **
Lines(BS10C0)*environments	[64]	1.4	3.3
Lines(BS10C13)*environments	[64]	2.1 *	3.7 *
Lines(BS11C0)*environments	[41]	2.9 **	4.9 **
Lines(BS11C13)*environments	[64]	1.6	2.0
Error (b) (pooled)	466	1.5	2.5
Total	947		

significant for grain yield and root lodging, and significant for grain moisture. The effects of environments are significant or highly significant for all traits measured. Differences among lines within each population are highly significant for all traits with the exception of root lodging, for which only the lines within BS11C0 mean square is significant.

Normality of random S_1 line distributions

Shapiro-Wilk (W), skewness, and kurtosis coefficients, used to assess normality of each random S_1 line mean distribution, are presented in Table 27, with histograms and normal curves shown in Appendix C. The null hypothesis that lines are random samples from a normal distribution is valid at a 95 percent confidence level for all populations for grain yield and plant height, and for ear height with the exception of BS10C13 due to an elongated lower tail of the distribution. The hypothesis is rejected for BS10C0, BS11C0 and BS11C13 for grain moisture, and for root lodging for all populations due to elongated upper tails and longer tails than for normal distributions with the same standard deviations. Stalk lodging means do not fit normal distributions for BS10C0, BS10C13, and BS11C13, as distributions have a flat-topped characteristic. The hypothesis is also rejected for days to mid-anthesis and mid-silk in BS10C0 and days to mid-silk in BS11C13, as a result of elongated upper tails and longer tails than for normal distributions with the same standard deviations.

Indirect effects of FR on BS10(S_1) and BS11(S_1)

Indirect effects of FR on the inbred *per se* populations, as measured from the performance of random lines, have generally been positive (Table 23). Improvements

Table 27. Shipiro-Wilk (W) coefficients for normality and coefficients of skewness and kurtosis for 65+ random S1 maize lines for each of eight traits.

Trait	Population	Shipiro-Wilk W	Coefficient of skewness	Coefficient of kurtosis
Grain yield (q ha ⁻¹)	BS10CO	0.99	0.24	-0.41
	BS10C13	0.98	0.12	-0.61
	BS11C0	0.98	-0.18	-0.43
	BS11C13	0.99	0.01	-0.02
Grain moisture (%)	BS10CO	0.94 **	0.77	0.13
	BS10C13	0.97	0.50	-0.28
	BS11C0	0.93 *	0.97	1.00
	BS11C13	0.95 **	0.65	2.57
Root lodging (%)	BS10CO	0.52 **	3.45	13.40
	BS10C13	0.5 **	3.91	18.77
	BS11C0	0.35 **	5.71	34.97
	BS11C13	0.71 **	2.13	4.99
Stalk lodging (%)	BS10CO	0.96 *	-0.19	-1.06
	BS10C13	0.90 **	0.83	-0.42
	BS11C0	0.98	0.29	0.16
	BS11C13	0.96 *	0.25	-0.99
Plant height (cm)	BS10CO	0.99	0.06	-0.09
	BS10C13	0.97	-0.44	-0.01
	BS11C0	0.98	0.12	-0.66
	BS11C13	0.98	-0.51	1.19
Ear height (cm)	BS10CO	0.98	0.42	0.17
	BS10C13	0.97 *	-0.68	0.24
	BS11C0	0.98	0.31	-0.49
	BS11C13	0.98	-0.09	-0.48
Days to mid-anthesis	BS10CO	0.90 **	1.14	2.21
	BS10C13	0.96	0.45	0.59
	BS11C0	0.95	0.54	-0.30
	BS11C13	0.99	0.11	0.16
Days to mid-silk	BS10CO	0.90 **	1.33	2.40
	BS10C13	0.98	0.16	-0.54
	BS11C0	0.98	0.16	-0.37
	BS11C13	0.95 *	0.79	0.67

† BS11C0 maize population statistics represent 42 random S1 lines

have been made for grain yield, root lodging, stalk lodging, days to mid-anthesis, and days to mid-silk in BS10(S₁), and for all measured traits with the exception of plant height in BS11(S₁). Per cycle grain yield increases equal 2.6 and 2.7 q ha⁻¹ for BS10(S₁) and BS11(S₁), respectively.

Effects of FR on variance in BS10 and BS11

Estimates of variance for grain yield for BS10 and BS11, based on variation among S₁ lines, suggest a lack of evidence for a decrease in *per se* genetic variation as a result of FR (Table 28). Genetic variance estimates increase from 42.1 to 64.7 and 58.5 to 60.3 in BS10 and BS11, respectively, although changes are not significant.

Corresponding changes occurred in genotype by environment interaction variance.

Heritability estimates increase from 0.75 to 0.76 in BS10, but decrease from 0.82 to 0.77 in BS11.

Estimates for other selected traits generally indicate a loss of genetic variance as a result of selection, with significant decreases for root lodging in BS11 and for grain moisture in both populations. Heritabilities are generally high for grain yield, grain moisture, and stalk lodging. Estimates range from 0.75 to 0.82 for grain yield, 0.82 to 0.92 for grain moisture, 0.02 to 0.47 for root lodging, and 0.50 to 0.76 for stalk lodging. The intervals around root lodging heritability estimates defined by their standard errors include zero for all populations, with the exception of BS11C0.

Genetic variability estimates for non-selected traits indicate significant losses of variability for all traits in both populations, with the exception of plant and ear height in BS11 (Table 29). A non-significant increase is evident in BS11 for plant height genetic

Table 28. Estimates of genotypic and genotype by environment variance components and heritabilities for selected maize traits, shown with their standard errors.

Trait	Population	$\sigma^2_G \pm$ standard error	$\sigma^2_{GE} \pm$ standard error	$h^2 \pm$ standard error
Grain yield (q ha ⁻¹)	BS11C0	58.499±15.538	5.074±5.533	0.824±0.219
	BS11C13	60.279±14.012	16.434±6.451	0.769±0.179
	Change†	1.780	11.360	
	BS10C0	42.085±10.123	8.724±5.144	0.747±0.180
	BS10C13	64.667±15.168	20.370±7.123	0.763±0.179
	Change	22.582	11.647	
Grain moisture (%)	BS11C0	3.753±0.880	0.398±0.136	0.923±0.216
	BS11C13	0.586±0.127	0.035±0.048	0.816±0.177
	Change	-3.167 *‡	-0.363 *	
	BS10C0	1.832±0.350	0.113±0.061	0.915±0.175
	BS10C13	1.004±0.207	0.115±0.062	0.854±0.176
	Change	-0.828 *	0.003	
Root lodging (%)	BS11C0	8.951±4.597	18.367±4.278	0.474±0.244
	BS11C13	0.031±0.429	1.987±0.609	0.018±0.244
	Change	-8.921 *	-16.380 *	
	BS10C0	0.132±0.288	0.737±0.395	0.107±0.233
	BS10C13	0.115±0.160	-0.288±0.226	0.164±0.227
	Change	-0.016	-1.026 *	
Stalk lodging (%)	BS11C0	305.994±88.723	131.744±40.896	0.764±0.222
	BS11C13	203.775±54.348	130.828±32.924	0.684±0.183
	Change	-102.219	0.916	
	BS10C0	144.590±41.654	104.274±28.337	0.642±0.185
	BS10C13	108.263±41.856	156.991±37.453	0.503±0.194
	Change	-36.327	52.717	

† Equals C13 variance minus C0 variance.

‡Significance is indicated when intervals around C0 and C13 variance components defined by standard errors do not overlap.

Table 29. Estimates of genotypic and genotype by environment variance components and heritabilities for non-selected maize traits, shown with their standard errors.

	Population	$\sigma^2_G \pm$ standard error	$\sigma^2_{GE} \pm$ standard error	$h^2 \pm$ standard error
Plant height (cm)	BS11C0	172.956 \pm 41.704	-4.018 \pm 8.840	0.899 \pm 0.217
	BS11C13	200.046 \pm 37.571	-12.409 \pm 6.002	0.929 \pm 0.175
	Change†	27.090	-8.391	
	BS10C0	254.150 \pm 48.552	4.603 \pm 8.730	0.915 \pm 0.175
	BS10C13	117.837 \pm 25.097	5.662 \pm 8.905	0.829 \pm 0.177
	Change	-136.313 *‡	1.059	
Ear height (cm)	BS11C0	150.521 \pm 35.836	5.968 \pm 6.644	0.910 \pm 0.217
	BS11C13	102.642 \pm 19.970	-0.970 \pm 4.299	0.899 \pm 0.175
	Change	-47.879	-6.938	
	BS10C0	158.879 \pm 31.150	14.129 \pm 6.814	0.893 \pm 0.175
	BS10C13	76.505 \pm 15.262	-2.901 \pm 3.988	0.879 \pm 0.175
	Change	-82.374 *	-17.030 *	
Days to mid-anthesis	BS11C0	4.330 \pm 1.104	0.706 \pm 0.320	0.855 \pm 0.218
	BS11C13	2.576 \pm 0.523	0.045 \pm 0.149	0.865 \pm 0.176
	Change	-1.754 *	-0.661 *	
	BS10C0	2.749 \pm 0.545	-0.040 \pm 0.135	0.884 \pm 0.175
	BS10C13	1.626 \pm 0.388	0.312 \pm 0.193	0.752 \pm 0.179
	Change	-1.123 *	0.352 *	
Days to mid-silk	BS11C0	5.211 \pm 1.413	1.180 \pm 0.534	0.810 \pm 0.220
	BS11C13	2.736 \pm 0.571	-0.261 \pm 0.194	0.845 \pm 0.176
	Change	-2.475 *	-1.441 *	
	BS10C0	5.593 \pm 1.126	0.375 \pm 0.298	0.872 \pm 0.176
	BS10C13	2.160 \pm 0.562	0.591 \pm 0.334	0.699 \pm 0.182
	Change	-3.432 *	0.216	

† Equals C13 variance minus C0 variance.

‡Significance is indicated when intervals around C0 and C13 variance components defined by standard errors do not overlap.

variance, while the estimate for ear height shows a non-significant decrease. Heritability estimates are high for all four traits, ranging from 0.83 to 0.93 for plant height, 0.88 to 0.91 for ear height, 0.75 to 0.88 for days to mid-anthesis, and 0.70 to 0.87 for days to mid-silk. With the exceptions of plant height and days to mid-anthesis and mid-silk in BS11, heritability estimates decrease from C0 to C13 populations for all non-selected traits.

DISCUSSION

Data from this evaluation indicate significant ($\text{prob}F < 0.05$) improvement over 13 cycles of FR in BS10/BS11 for grain yield and moisture, stalk lodging, plant and ear height, and days to mid-anthesis and mid-silk. Indirect effects of selection on the *per se* populations include significant improvement for grain yield and stalk lodging in BS10 and grain yield and moisture, plant and ear height and days to mid-anthesis and mid-silk in BS11. Correlated changes are evident for most traits in their respective inbred populations. Results are similar to those of evaluations over early cycles of FR in BS10 and BS11, indicating improvement in selected traits while improving earliness in the population cross (Obilana et al. 1979; Eyherabide and Hallauer, 1991a). Improvements in maturity related traits in the population cross can be attributed primarily to favorable changes in the BS11 parent population.

Increases in grain yield include a direct response of 2.2 percent per cycle in the population cross, and indirect responses of 3.3 and 1.2 percent per cycle in BS10 and BS11, respectively. These results conflict with earlier evaluations of progress in BS10 and BS11, which indicated greater response rates in the population cross than either of the *per se* populations (Hallauer, 1984, Eyherabide and Hallauer, 1991a). Greater response in the hybrid population is generally expected for most genetic models based on simulations; the exceptions are models involving only additive effects or additive by additive epistasis, or a partially dominant model in which one of the parent populations has a high initial frequency of favorable alleles (Peiris, 2001). While response rates in *per se* populations are similar to the nonlinear 3.0 percent per cycle increase in BS10 and

linear 1.6 percent per cycle improvement in BS11 for grain yield reported by Eyherabide and Hallauer (1991a), their results suggest nearly all of the improvement in BS10 occurred in the first four cycles of selection, while results of this evaluation indicate only a 1.6 percent per cycle improvement over the first nine selection cycles, with most of the improvement between C9 and C11. Population cross performance over eight cycles of selection was previously reported at 6.5 percent per cycle (Eyherabide and Hallauer, 1991a). As simulations indicate expected decreases in *per se* performance with direct selection on F_1 performance in reciprocal selection methods under overdominance models (Cress, 1967; Peiris, 2001), the consistent increase in yield for BS10 and BS11 provides evidence that overdominance does not have a major role for grain yield heterosis between these populations.

Results over the first nine selection cycles for grain yield based on data in this study are consistent with results previously reported from C0 to C8 (Eyherabide and Hallauer, 1991a), though only the C0 population is common to both evaluations. A 4.6 percent per cycle increase in this study for the population cross through C9, as well as increases of 1.6 percent in BS10 and 1.6 percent in BS11 parent populations, compared with previous results of 6.5, 3.0, and 1.6 percent per cycle improvements through C8 in BS10/BS11, BS10, and BS11, respectively (Eyherabide and Hallauer, 1991a). Linear models account for 0.92, 0.82, and 0.91 percent of the variation observed among means within those same populations through C9, while only 0.60 percent of the variation in the population cross is explained by a linear model over the first 13 cycles. Only data for BS11 fit a linear model from C0 to C13.

Mid-parent heterosis estimates increase from 10.6 percent in C0 to 33.5 percent in C9, followed by a decrease to 9.3 in C11, while high-parent heterosis is estimated at 7.2, 29.8, and 5.0 in the C0, C9, and C11 populations, respectively. Increases in heterosis in early cycles are consistent with results of Obilana et al. (1979), indicating increases from 10.8 percent in C0 to 16.5 percent in C3 for mid-parent heterosis, compared with a change from 10.6 to 19.1 percent over the same cycles in this study. Estimates of heterosis in the original (C0) populations are similar to those reported by Obilana et al. (1979) and Hallauer (1984), but higher than those by Eyherabide and Hallauer (1991a). Results from Eyherabide and Hallauer (1991a) through C8 indicated changes in mid-parent heterosis from 2.5 to 39.7 percent and in high-parent heterosis from -5.5 to 34.2 percent, although trends across cycles were not as consistent as through C9 in the current study. Increases in heterosis between BS10 and BS11 “suggest that reciprocal full-sib selection either caused changes in the frequency of genes with dominant effects in a different set of loci for each population, or selected different isoalleles with dominant effects in each population” (Eyherabide and Hallauer, 1991a). Levels of heterosis are affected by allele frequencies, which are expected to change as a result of selection and drift.

Inbreeding depression trends for grain yield were erratic for both *per se* populations and their F_1 . Maximum contributions of loci to inbreeding depression occur at $p = q = 0.5$ (Falconer and Mackay, 1996), with no contribution from loci fixed for one allele by selection or drift. Lower *per se* population inbreeding depression levels in C13 than in C0 are consistent with results from RRS in BSSS and BSCB1 (Benson and

Hallauer, 1994) over nine cycles and in BS10 and BS11 over eight cycles (Eyherabide and Hallauer, 1991a), possibly due to fixation or allele frequency changes away from $p = q = 0.5$ at loci involved in grain yield. An increasing trend in inbreeding depression percentage is evident in the population cross from C0 to C7, while percentages in C11 and C13 are lower than that of the original population. Increased inbreeding depression in the population cross would lead me to suggest an increase in heterozygosity from C0 to C7, which may arise through selection of favorable alleles at different loci in each of the parent populations.

Selection effects on stalk lodging means seem to reflect changing emphases on traits other than grain yield over the duration of the selection program. Early selections giving considerable weight to lodging traits, both among S_0 plants and full-sib families (Hallauer, 1984), along with selection on European corn borer ratings on full-sib families and stalk quality of S_1 lines themselves in C2 (Obilana et al. 1979), correlated with rapid improvements in stalk lodging means from C0 to C3 (Figure 5). Results indicate much of this improvement was lost from C0 to C5, which is consistent with earlier evaluations (Hallauer, 1984). However, emphasis on standability in later cycles, particularly the inclusion of lodging traits and grain moisture in heritability weighted selection indices that began in C6, has improved standability in *per se* populations and their F_1 through C13. An increase in stalk lodging was evident in BS10 and the population cross from C9 to C11, with a slight decrease in BS11, bringing means of BS10 and the population cross near that of BS11, the population which had greater incidence of stalk lodging for most cycles evaluated in this research.

No significant differences are evident among entries for any population for root lodging. This is likely due to a lack of conditions favorable for root lodging during the 2000 growing season and not a true lack of variation among entries for the trait, as previous results indicated a significant decrease in root lodging in BS11 as a result of eight FR cycles (Eyherabide and Hallauer, 1991a). High levels of stalk lodging may have contributed to the lower values for root lodging in this study, as plants both root lodged and stalk lodged were recorded as stalk lodged.

Improvements for non-selected traits, significant in BS11 and BS10/BS11, may be due to correlations with traits under selection, although some selection on S_0 plants was conducted for earlier flowering (Obilana et al. 1979). Relatively high heritabilities for flowering traits is evidence that selection among single plants in the breeding nursery to produce the full-sib families was effective.

Evaluations of random S_1 line performance for BS10C0, BS10C13, BS11C0, and BS11C13 indicate decreases in genetic variability occurred over 13 cycles of FR. Exceptions are grain yield in BS10 and BS11 and plant height in BS11. While genetic variance estimates were nearly equal for BS11C0 and BS11C13, a large, nearly significant increase in variability occurred in BS10. While the difference was not significant based on overlapping intervals around the variance estimates determined by their standard errors, the apparent increase contradicts the report of a non-significant decrease in grain yield genetic variance in BS10 through C10 (Frank and Hallauer, 1999). Decreases in genetic variance estimates for other traits observed in this study are generally consistent with earlier results (Frank and Hallauer, 1999). Standard error

defined intervals around genetic variance estimates for root lodging in BS11C13 and both BS10 populations include zero. Heritabilities were moderate to high for all traits with the exception of root lodging, with estimates for grain yield higher (from 0.75 to 0.82) than expected for results based on two replications at two environments.

Results from both experiments one and two defy explanation by genetic changes associated with selection alone. Several focus on changes from cycle nine to cycle 11. Results suggesting non-selection related explanations for observed responses through 13 cycles of FR include:

- 1) A significant decrease in mean grain yield in BS10/BS11 of 7.5 q ha^{-1} from C9 to C11, although variance estimates through C10 (Frank and Hallauer, 1999) provide no evidence for reduced expectations of genetic gain per cycle.
- 2) A sharp increase in mean grain yield in BS10 of 8.6 q ha^{-1} from C9 to C11, which is inconsistent with increases observed in earlier cycles.
- 3) A decrease in mid-parent heterosis, from 33.5 to 9.3 percent, and in high-parent heterosis, from 29.8 to 5.0 percent, between C9 and C11, following strong trends toward increased heterosis from C0 to C9.
- 4) An increase in stalk lodging percentage in BS10 and BS10/BS11, combined with a slight decrease in BS11, making means for all populations nearly equal.
- 5) More similar mean estimates in nearly all cases in both inbred and noninbred BS10, BS11, and F_1 populations in C11 than for any other cycle evaluated.

- 6) An increase in genetic variability from 42.1 in C0 to 64.7 in C13 for grain yield in BS10, contradictory to results from C0 to C10 (Frank and Hallauer, 1999).

While a change in the rate of improvement in a population cross is expected in later cycles based on simulation studies (Peiris, 2001), a decrease in the mean of the primary trait for selection is not expected under any genetic model. The explanation proposed here is a contamination of the BS10 population with BS11 material during intermating to form either the C10 or C11 population. Expected results of an addition of BS11 germplasm into the BS10 population include an increase in BS10 performance, a decrease in population cross performance, a decrease in heterosis between BS10 and BS11, an increase in genetic variability in BS10, and means of all populations becoming more similar for each trait.

CONCLUSIONS

Thirteen cycles of FR were successful for improvement of BS10, BS11, and the population cross for selected and non-selected traits. Genetic variability in the parent populations decreased for most traits, with the exception of grain yield, which increased slightly in BS11 and to a greater degree in BS10. Continued progress for grain yield, therefore, should be possible in BS10/BS11. The nature of the response and changes in variability, however, provide evidence for a possible contamination of the BS10 population with BS11 material between cycles nine and 11.

Results through cycle nine demonstrate a greater rate of improvement for grain yield, the primary trait for selection, in the population cross than in either *per se* population. A strong increasing trend for heterosis for grain yield between the two populations indicates a progression toward greater heterozygosity in the population cross. Improvements per cycle for grain yield measure 4.6 percent in the population cross, 1.6 percent in BS10, and 1.6 percent in BS11.

Future research is necessary to determine the nature and timing of potential contamination of the BS10 parent population. Use of field evaluations to determine precisely the first cycle affected is necessary to provide information for future decisions and to interpret these and earlier results, including assessments of variability through cycle 10 reported by Frank and Hallauer (1999). Use of genetic markers may allow for a determination of the nature of the contamination by identifying BS11 or other non-BS10 alleles in the BS10 population.

Results here suggest two possible options for continued long-term selection. The first is to continue with the cycle 15 populations in spite of the possible earlier contamination, allowing the use of the BS11 tester on BS10 to again improve heterosis between the two populations. The second, which would allow for future theoretical studies on long-term changes in allele frequencies, genetic gain, and genetic variability, would require beginning selection again with the last uncontaminated populations, potentially the cycle nine or ten populations.

**APPENDIX A: EXPERIMENT ONE ENTRY MEANS AT
INDIVIDUAL ENVIRONMENTS FOR GRAIN YIELD (YLD),
GRAIN MOISTURE (MST), ROOT LODGING (RL), STALK
LODGING (SL), PLANT HEIGHT (PH), EAR HEIGHT (EH), AND
DAYS TO MID-ANTHESIS (DTA) AND MID-SILK (DTS)**

Appendix A1. Entry means at Ames, Iowa.

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm	DTA	DTS
BS10C0	50.30	16.55	0.00	53.57	243.00	135.50	84.00	86.00
BS10C0	56.15	17.45	0.00	39.26	222.50	120.50	85.00	88.00
BS10(FR)C3	58.22	17.70	0.00	26.93	230.00	133.50	83.50	87.00
BS10(FR)C5	44.86	17.15	0.00	74.74	233.50	127.50	83.00	86.00
BS10(FR)C7	58.07	16.90	0.00	28.24	234.00	123.50	85.50	88.00
BS10(FR)C9	54.14	17.05	0.00	30.91	227.00	119.00	87.50	89.50
BS10(FR)C11	60.60	17.10	0.00	40.18	229.50	124.50	84.00	86.50
BS10(FR)C13	61.42	18.50	0.00	31.82	233.00	133.00	83.50	87.00
BS10(FR)C13	58.75	18.25	0.00	35.58	239.00	131.00	83.00	85.00
BS11C0	41.55	20.65	0.00	56.12	255.00	151.00	88.50	91.50
BS11C0	61.64	20.60	0.00	34.82	259.00	157.00	85.00	91.50
BS11(FR)C3	50.23	20.25	0.00	30.36	234.50	129.50	86.00	87.00
BS11(FR)C5	57.09	18.70	0.00	58.38	237.50	132.50	82.50	85.00
BS11(FR)C7	69.74	18.25	0.00	23.28	226.00	110.50	85.00	87.00
BS11(FR)C9	64.40	19.10	0.00	36.61	260.00	137.00	82.50	86.00
BS11(FR)C11	58.55	17.80	0.00	39.82	237.00	139.50	84.00	86.00
BS11(FR)C13	43.25	15.70	0.90	41.41	234.50	127.00	83.50	85.00
BS11(FR)C13	59.45	15.70	0.00	62.46	247.00	132.50	84.50	85.50
BS10CO/BS11CO	62.68	18.95	0.00	63.02	253.50	142.00	85.00	87.00
BS10CO/BS11CO	76.09	18.75	0.00	42.28	257.50	151.00	84.00	88.50
BS10(FR)C3/BS11(FR)C3	66.13	17.85	0.00	42.29	243.00	136.50	82.50	85.00
BS10(FR)C5/BS11(FR)C5	67.32	17.35	0.00	68.75	240.50	133.50	84.00	86.00
BS10(FR)C7/BS11(FR)C7	78.29	17.10	0.00	29.47	239.50	131.00	83.50	86.00
BS10(FR)C9/BS11(FR)C9	82.41	17.40	0.00	33.93	254.00	136.00	83.00	85.00
BS10(FR)C11/BS11(FR)C11	72.70	17.30	0.00	44.55	245.50	133.00	83.00	86.00
BS10(FR)C13/BS11(FR)C13	71.20	16.60	0.00	38.06	242.00	126.00	84.00	85.00
BS10(FR)C13/BS11(FR)C13	80.66	17.00	0.00	38.40	236.50	128.00	82.00	84.00
BS10C0(S1)	27.10	17.10	0.00	36.11	208.50	115.50	85.00	88.00
BS10C0(S1)	26.62	16.15	0.00	50.00	216.00	121.50	84.00	87.50
BS10(FR)C3(S1)	20.52	16.95	0.00	30.79	201.50	109.00	84.00	88.50
BS10(FR)C5(S1)	36.03	17.40	0.00	66.62	214.00	122.00	85.50	89.00
BS10(FR)C7(S1)	25.83	18.65	0.00	19.05	228.50	119.50	86.50	89.50
BS10(FR)C9(S1)	22.55	16.35	0.00	19.64	208.50	100.50	86.50	89.00
BS10(FR)C11(S1)	35.33	18.40	0.00	28.65	226.00	119.50	86.00	88.50
BS10(FR)C13(S1)	38.92	18.45	0.00	24.72	229.50	120.50	85.00	86.50
BS10(FR)C13(S1)	36.00	18.65	0.00	18.58	222.00	122.00	86.00	87.50
BS11C0(S1)	22.61	18.95	0.00	27.19	216.50	119.50	87.50	93.50
BS11C0(S1)	25.72	19.95	0.00	46.57	233.00	135.50	88.50	91.00
BS11(FR)C3(S1)	23.62	17.25	0.00	27.89	214.00	109.50	86.00	89.00
BS11(FR)C5(S1)	27.56	18.95	0.00	75.30	222.00	125.50	86.00	90.50
BS11(FR)C7(S1)	28.28	19.05	0.00	32.16	217.50	118.00	88.50	92.50
BS11(FR)C9(S1)	31.23	18.15	0.00	33.75	224.00	124.00	85.00	89.50
BS11(FR)C11(S1)	27.95	17.80	1.02	49.47	236.50	129.00	85.50	90.00
BS11(FR)C13(S1)	24.15	16.40	0.00	30.13	221.50	111.00	86.00	87.50
BS11(FR)C13(S1)	25.82	17.00	0.00	40.18	222.00	110.50	84.50	86.50

Appendix A1. (continued)

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm	DTA	DTS
(BS10CO/BS11CO)(S1)	37.12	18.80	0.00	33.16	223.00	117.00	85.00	90.50
(BS10CO/BS11CO)(S1)	34.14	18.80	0.00	44.89	221.50	119.50	85.00	90.50
(BS10(FR)C3/BS11(FR)C3)(S1)	42.72	16.75	0.00	33.03	235.00	129.00	84.00	86.00
(BS10(FR)C5/BS11(FR)C5)(S1)	37.76	16.55	0.00	36.12	223.50	116.00	83.50	84.00
(BS10(FR)C7/BS11(FR)C7)(S1)	40.53	16.80	0.00	29.81	225.50	121.50	85.00	88.00
(BS10(FR)C9/BS11(FR)C9)(S1)	40.06	16.60	0.00	31.48	232.00	120.00	84.50	88.50
(BS10(FR)C11/BS11(FR)C11)(S1)	35.05	17.80	0.00	40.69	223.00	120.50	86.00	89.00
(BS10(FR)C13/BS11(FR)C13)(S1)	35.52	17.20	0.00	26.15	224.00	106.00	84.50	87.50
(BS10(FR)C13/BS11(FR)C13)(S1)	40.04	16.70	0.00	32.30	223.00	109.50	86.00	87.00
Mean of all entries	46.57	17.76	0.04	39.07	231.22	125.43	84.83	87.69
Standard error of an entry mean	6.57	0.58	0.55	11.07	7.89	5.36	0.87	1.13
LSD(0.05)	18.65	1.65	0.52	31.41	22.37	15.20	2.48	3.21

Appendix A2. Entry means at Ankeny, Iowa.

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm	DTA	DTS
BS10C0	43.06	14.95	0.90	29.46	213.50	114.00	76.50	80.00
BS10C0	47.57	14.75	3.64	13.84	201.50	105.50	77.00	79.00
BS10(FR)C3	48.66	14.30	0.00	10.97	197.00	106.00	77.50	80.00
BS10(FR)C5	60.05	14.90	0.00	9.87	206.00	106.00	77.00	81.00
BS10(FR)C7	54.33	14.45	0.00	9.10	220.00	114.50	79.00	81.00
BS10(FR)C9	59.07	14.75	0.00	13.95	221.00	111.50	77.50	79.00
BS10(FR)C11	67.17	15.20	0.00	12.58	221.50	117.00	78.00	80.00
BS10(FR)C13	67.50	15.80	0.90	9.82	220.00	118.50	77.50	78.00
BS10(FR)C13	64.97	15.60	0.90	10.71	216.00	117.00	77.00	80.00
BS11C0	58.11	16.40	0.90	29.76	243.50	142.50	80.00	84.00
BS11C0	49.06	16.40	1.79	25.90	235.50	139.00	80.00	86.00
BS11(FR)C3	62.85	15.50	0.90	12.62	224.50	117.50	78.00	80.00
BS11(FR)C5	53.87	15.60	0.00	25.00	223.50	122.00	78.00	80.00
BS11(FR)C7	56.20	15.40	0.98	20.78	217.00	111.00	79.00	80.00
BS11(FR)C9	50.49	15.75	1.84	11.07	231.00	121.50	79.00	81.00
BS11(FR)C11	65.12	15.40	0.00	23.22	233.00	127.00	79.00	80.00
BS11(FR)C13	71.57	14.80	0.90	5.36	235.00	124.00	78.00	80.00
BS11(FR)C13	60.60	14.50	3.85	11.18	235.00	124.50	78.00	81.00
BS10CO/BS11CO	54.89	16.05	0.00	25.46	236.50	134.50	80.00	81.00
BS10CO/BS11CO	62.80	15.25	1.79	20.54	240.50	135.50	78.00	81.00
BS10(FR)C3/BS11(FR)C3	62.58	15.20	0.91	15.30	217.00	122.50	79.00	80.00
BS10(FR)C5/BS11(FR)C5	70.34	15.00	2.83	22.04	227.00	121.00	78.00	80.00
BS10(FR)C7/BS11(FR)C7	64.80	15.10	0.90	24.33	235.50	130.00	78.50	80.00
BS10(FR)C9/BS11(FR)C9	73.33	15.30	0.00	11.61	226.00	118.00	79.00	80.00
BS10(FR)C11/BS11(FR)C11	69.69	15.50	0.00	18.75	224.00	118.00	78.00	79.00
BS10(FR)C13/BS11(FR)C13	68.01	15.20	0.98	7.59	231.00	124.00	78.50	80.00
BS10(FR)C13/BS11(FR)C13	79.78	15.10	0.90	8.17	220.50	112.50	77.50	79.00
BS10C0(S1)	25.23	14.50	1.11	22.01	191.00	100.00	80.00	82.00
BS10C0(S1)	28.65	14.90	0.00	26.92	201.50	106.00	78.00	82.00
BS10(FR)C3(S1)	34.50	14.65	1.09	22.05	198.00	111.00	78.00	82.00
BS10(FR)C5(S1)	33.77	14.40	0.95	21.12	194.50	108.50	81.00	82.00
BS10(FR)C7(S1)	36.32	14.20	0.98	12.41	202.00	105.50	80.00	82.00
BS10(FR)C9(S1)	25.75	14.60	1.07	13.53	193.00	97.50	78.50	82.00
BS10(FR)C11(S1)	40.31	14.50	1.82	19.91	197.00	103.00	80.00	82.00
BS10(FR)C13(S1)	42.35	15.35	1.85	23.61	211.50	111.50	79.50	80.00
BS10(FR)C13(S1)	46.20	15.25	0.00	9.61	213.50	115.00	79.00	80.00
BS11C0(S1)	18.96	16.80	0.98	15.58	207.00	121.00	80.00	86.00
BS11C0(S1)	25.97	15.65	2.78	7.62	206.00	112.50	80.00	86.00
BS11(FR)C3(S1)	35.89	15.85	0.96	5.86	196.00	97.00	80.00	81.00
BS11(FR)C5(S1)	36.70	15.85	1.79	15.44	211.50	119.00	77.50	83.00
BS11(FR)C7(S1)	34.03	15.80	1.82	20.00	198.00	105.50	81.00	83.00
BS11(FR)C9(S1)	36.97	15.85	0.98	18.26	213.00	109.50	81.00	84.00
BS11(FR)C11(S1)	38.15	15.05	1.02	14.54	207.00	105.50	81.00	84.00
BS11(FR)C13(S1)	41.54	14.30	0.00	16.13	215.50	112.00	80.00	83.00
BS11(FR)C13(S1)	41.41	14.50	2.85	13.63	212.50	104.50	79.00	81.00

Appendix A2. (continued)

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm	DTA	DTS
(BS10CO/BS11CO)(S1)	27.88	15.60	0.00	19.39	201.00	114.50	81.00	85.00
(BS10CO/BS11CO)(S1)	23.19	14.95	1.82	24.00	214.50	116.50	80.00	83.00
(BS10(FR)C3/BS11(FR)C3)(S1)	38.80	15.40	0.90	18.41	207.00	107.00	80.00	81.00
(BS10(FR)C5/BS11(FR)C5)(S1)	34.47	14.70	6.71	14.41	198.50	106.00	79.00	81.00
(BS10(FR)C7/BS11(FR)C7)(S1)	41.39	15.65	1.81	9.05	217.50	113.00	80.00	82.00
(BS10(FR)C9/BS11(FR)C9)(S1)	42.48	15.10	0.00	14.05	217.00	112.00	80.00	81.00
(BS10(FR)C11/BS11(FR)C11)(S1)	43.66	15.40	2.78	19.11	209.50	115.00	81.00	82.00
(BS10(FR)C13/BS11(FR)C13)(S1)	43.00	15.20	0.96	13.32	202.50	106.50	79.00	82.00
(BS10(FR)C13/BS11(FR)C13)(S1)	40.51	14.65	0.95	12.86	194.00	104.50	79.00	81.00
Mean of all entries	48.23	15.20	1.18	16.33	214.49	114.71	78.98	81.35
Standard error of an entry mean	3.65	0.29	1.29	4.11	6.43	4.59	1.00	1.16
LSD(0.05)	10.34	0.84	3.65	11.67	18.24	13.02	2.85	3.30

Appendix A3. Entry means at Carroll, Iowa.

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm
BS10C0	45.39	16.20	0.00	72.38	236.00	124.00
BS10C0	40.49	16.40	0.98	42.93	225.50	125.00
BS10(FR)C3	36.96	15.90	2.80	59.01	224.00	126.00
BS10(FR)C5	41.39	16.35	0.00	59.05	230.00	126.50
BS10(FR)C7	34.41	14.85	0.00	60.02	225.50	119.00
BS10(FR)C9	47.42	16.40	0.00	38.99	234.50	125.00
BS10(FR)C11	60.44	16.25	0.00	42.55	233.00	125.50
BS10(FR)C13	55.71	16.45	0.00	25.77	226.00	117.50
BS10(FR)C13	63.93	16.55	0.00	30.85	216.00	121.50
BS11C0	38.70	17.90	0.91	63.90	254.50	143.50
BS11C0	40.30	17.40	5.66	58.08	235.50	136.00
BS11(FR)C3	50.98	15.90	0.96	60.93	229.50	125.00
BS11(FR)C5	44.68	16.50	5.00	74.91	237.50	138.00
BS11(FR)C7	42.90	16.40	6.26	71.75	232.00	131.00
BS11(FR)C9	53.64	17.25	1.96	59.70	247.50	135.50
BS11(FR)C11	39.64	16.50	0.00	52.40	244.50	132.50
BS11(FR)C13	50.64	14.20	1.00	70.34	238.50	123.50
BS11(FR)C13	54.26	15.40	0.86	60.22	243.00	129.50
BS10C0/BS11C0	43.50	16.35	3.06	68.11	247.50	139.00
BS10C0/BS11C0	44.54	16.35	0.95	66.16	230.50	128.00
BS10(FR)C3/BS11(FR)C3	48.20	16.00	0.00	33.39	234.50	135.50
BS10(FR)C5/BS11(FR)C5	52.71	16.70	1.70	50.64	235.50	128.50
BS10(FR)C7/BS11(FR)C7	64.60	16.85	1.70	68.45	251.00	136.00
BS10(FR)C9/BS11(FR)C9	59.48	16.40	0.00	44.30	243.00	129.00
BS10(FR)C11/BS11(FR)C11	58.10	16.55	0.00	52.20	225.50	125.00
BS10(FR)C13/BS11(FR)C13	66.58	15.60	0.00	19.83	239.50	129.00
BS10(FR)C13/BS11(FR)C13	50.84	16.15	0.00	36.50	244.00	134.00
BS10C0(S1)	25.55	17.05	1.00	57.96	209.50	110.50
BS10C0(S1)	26.66	16.85	0.00	68.43	200.00	114.50
BS10(FR)C3(S1)	29.56	16.20	0.98	70.24	204.00	116.50
BS10(FR)C5(S1)	27.33	16.35	3.00	71.32	208.00	114.00
BS10(FR)C7(S1)	35.87	16.50	1.39	50.65	214.00	118.00
BS10(FR)C9(S1)	30.66	16.10	0.93	62.11	212.00	110.50
BS10(FR)C11(S1)	38.52	16.60	0.96	47.34	218.00	117.00
BS10(FR)C13(S1)	39.12	16.45	0.00	36.15	217.00	115.00
BS10(FR)C13(S1)	36.24	16.35	0.00	45.90	220.00	120.00
BS11C0(S1)	24.96	18.10	1.07	57.72	218.50	120.50
BS11C0(S1)	23.18	17.85	1.02	59.63	228.50	139.00
BS11(FR)C3(S1)	26.56	16.20	1.04	58.21	212.00	120.00
BS11(FR)C5(S1)	32.58	16.70	3.13	75.00	219.50	125.50
BS11(FR)C7(S1)	27.32	17.25	0.00	56.25	224.00	123.50
BS11(FR)C9(S1)	27.12	17.05	1.79	55.31	235.00	126.00
BS11(FR)C11(S1)	32.50	16.30	0.91	47.71	227.00	121.00
BS11(FR)C13(S1)	29.85	14.60	2.13	57.06	222.50	117.00
BS11(FR)C13(S1)	27.05	14.80	1.73	61.07	216.50	116.50

Appendix A3. (continued)

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm
(BS10CO/BS11CO)(S1)	20.64	15.30	0.00	70.56	222.00	125.00
(BS10CO/BS11CO)(S1)	36.35	16.05	2.28	63.45	222.50	121.00
(BS10(FR)C3/BS11(FR)C3)(S1)	28.77	16.95	1.07	54.78	205.00	115.00
(BS10(FR)C5/BS11(FR)C5)(S1)	28.67	15.70	0.90	62.13	221.50	128.00
(BS10(FR)C7/BS11(FR)C7)(S1)	28.51	15.35	0.90	70.03	224.50	116.50
(BS10(FR)C9/BS11(FR)C9)(S1)	37.05	16.90	0.00	42.09	230.50	118.00
(BS10(FR)C11/BS11(FR)C11)(S1)	31.73	16.10	0.00	51.77	223.00	119.50
(BS10(FR)C13/BS11(FR)C13)(S1)	33.52	16.25	1.91	54.37	216.00	111.50
(BS10(FR)C13/BS11(FR)C13)(S1)	33.93	16.00	2.77	51.10	229.00	121.00
Mean of all entries	39.82	16.33	1.20	55.58	227.11	124.24
Standard error of an entry mean	5.22	0.45	1.62	8.28	5.49	4.24
LSD(0.05)	14.81	1.28	4.58	23.48	15.57	12.03

Appendix A4. Entry means at Rippey, Iowa.

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm
BS10C0	37.55	14.60	2.86	24.53	231.50	120.50
BS10C0	38.54	14.70	2.83	36.73	226.50	113.50
BS10(FR)C3	39.40	14.70	2.89	37.73	218.00	114.50
BS10(FR)C5	52.47	14.80	2.78	34.68	221.00	117.50
BS10(FR)C7	49.71	14.35	4.39	16.81	219.50	105.50
BS10(FR)C9	42.21	15.10	0.00	13.48	224.50	107.50
BS10(FR)C11	52.70	15.30	7.46	32.76	225.00	117.50
BS10(FR)C13	64.98	15.00	8.21	16.89	240.00	130.00
BS10(FR)C13	57.22	15.85	8.78	19.31	229.00	115.00
BS11C0	50.23	16.25	6.62	39.28	243.00	133.50
BS11C0	43.94	16.45	7.02	38.25	252.50	130.00
BS11(FR)C3	44.51	15.35	8.59	27.40	230.50	124.00
BS11(FR)C5	51.14	15.60	11.07	29.38	231.50	122.00
BS11(FR)C7	42.62	15.40	4.34	29.55	233.00	115.00
BS11(FR)C9	48.60	15.35	5.12	26.55	239.00	119.50
BS11(FR)C11	48.80	15.00	2.68	25.36	231.00	109.00
BS11(FR)C13	50.69	14.10	1.85	22.93	240.50	124.00
BS11(FR)C13	57.75	13.85	2.63	16.98	244.00	115.50
BS10C0/BS11C0	39.57	14.95	2.59	30.33	253.00	135.00
BS10C0/BS11C0	47.68	15.05	1.67	31.02	240.00	124.50
BS10(FR)C3/BS11(FR)C3	51.00	15.40	13.03	28.79	240.00	123.50
BS10(FR)C5/BS11(FR)C5	61.60	14.65	7.71	27.34	243.50	137.50
BS10(FR)C7/BS11(FR)C7	62.24	14.90	9.02	25.41	246.00	128.50
BS10(FR)C9/BS11(FR)C9	60.43	15.50	6.01	21.30	238.00	114.50
BS10(FR)C11/BS11(FR)C11	54.27	14.55	5.67	20.53	229.50	114.50
BS10(FR)C13/BS11(FR)C13	50.11	14.65	5.31	18.07	233.00	118.50
BS10(FR)C13/BS11(FR)C13	59.56	15.20	0.00	13.03	232.50	122.50
BS10C0(S1)	27.34	14.75	7.68	27.56	198.50	95.50
BS10C0(S1)	24.77	14.25	2.00	30.00	214.00	107.50
BS10(FR)C3(S1)	29.88	14.45	2.63	37.41	215.00	113.00
BS10(FR)C5(S1)	24.15	14.45	0.96	27.89	207.00	110.00
BS10(FR)C7(S1)	27.17	14.40	1.00	22.73	206.50	100.00
BS10(FR)C9(S1)	30.69	14.55	0.00	19.65	216.00	99.50
BS10(FR)C11(S1)	32.49	15.55	3.86	35.87	222.50	114.50
BS10(FR)C13(S1)	36.10	15.45	0.00	16.48	215.50	108.00
BS10(FR)C13(S1)	38.80	14.85	5.44	30.22	209.00	107.50
BS11C0(S1)	25.53	15.30	8.17	27.57	222.00	117.50
BS11C0(S1)	27.41	16.20	6.91	31.89	205.50	103.00
BS11(FR)C3(S1)	30.64	15.40	11.42	24.80	207.00	99.50
BS11(FR)C5(S1)	27.66	15.45	9.23	37.95	218.00	114.50
BS11(FR)C7(S1)	29.85	14.65	2.75	34.02	218.00	105.00
BS11(FR)C9(S1)	26.34	15.35	16.67	38.63	228.00	117.00
BS11(FR)C11(S1)	28.16	14.75	5.77	21.15	225.50	114.00
BS11(FR)C13(S1)	30.29	14.15	5.93	21.72	210.00	103.50
BS11(FR)C13(S1)	32.24	14.10	3.75	19.51	226.50	115.00

Appendix A4. (continued)

Population	YLD q ha ⁻¹	MST %	RL %	SL %	PH cm	EH cm
(BS10CO/BS11CO)(S1)	24.37	14.65	2.83	18.92	205.00	106.50
(BS10CO/BS11CO)(S1)	27.89	14.85	2.82	33.64	227.50	129.50
(BS10(FR)C3/BS11(FR)C3)(S1)	28.58	14.30	4.53	25.00	206.00	104.50
(BS10(FR)C5/BS11(FR)C5)(S1)	27.52	14.15	5.53	35.87	214.00	111.00
(BS10(FR)C7/BS11(FR)C7)(S1)	34.96	14.80	14.96	21.58	226.50	113.00
(BS10(FR)C9/BS11(FR)C9)(S1)	33.55	15.00	3.71	22.30	218.50	105.50
(BS10(FR)C11/BS11(FR)C11)(S1)	39.96	14.65	0.00	30.07	217.50	108.00
(BS10(FR)C13/BS11(FR)C13)(S1)	39.40	14.70	8.83	27.02	238.50	123.50
(BS10(FR)C13/BS11(FR)C13)(S1)	34.17	14.80	5.77	26.75	225.50	115.00
Mean of all entries	40.36	14.94	5.26	26.86	225.54	115.07
Standard error of an entry mean	4.29	0.32	3.37	5.18	6.94	5.65
LSD(0.05)	12.18	0.90	9.56	14.69	19.69	16.04

Appendix A5. Entry means at Fairfield, Iowa.

Population	YLD q ha ⁻¹	MST %	RL %	SL %
BS10C0	41.34	15.20	2.42	80.65
BS10C0	30.21	15.20	0.81	85.54
BS10(FR)C3	43.15	14.85	5.73	76.11
BS10(FR)C5	36.69	15.20	2.00	85.40
BS10(FR)C7	38.27	14.75	3.61	75.43
BS10(FR)C9	52.83	14.90	5.15	46.81
BS10(FR)C11	57.58	15.05	3.64	59.13
BS10(FR)C13	79.09	15.90	4.22	38.21
BS10(FR)C13	64.25	15.45	1.85	49.73
BS11C0	41.12	16.75	1.82	73.91
BS11C0	45.58	16.90	1.80	77.38
BS11(FR)C3	49.82	15.60	2.54	56.36
BS11(FR)C5	47.68	15.55	1.85	82.27
BS11(FR)C7	55.52	15.55	1.73	75.53
BS11(FR)C9	49.94	14.95	0.90	82.86
BS11(FR)C11	52.70	15.65	4.55	66.07
BS11(FR)C13	47.56	14.20	2.68	85.95
BS11(FR)C13	52.00	14.65	1.64	79.55
BS10CO/BS11CO	44.30	15.70	1.85	71.31
BS10CO/BS11CO	47.45	16.90	1.62	73.25
BS10(FR)C3/BS11(FR)C3	52.25	14.80	3.36	51.70
BS10(FR)C5/BS11(FR)C5	58.57	15.35	0.00	78.82
BS10(FR)C7/BS11(FR)C7	71.13	15.35	1.70	63.77
BS10(FR)C9/BS11(FR)C9	71.55	15.50	1.64	63.94
BS10(FR)C11/BS11(FR)C11	65.56	15.20	0.88	67.37
BS10(FR)C13/BS11(FR)C13	50.97	15.50	3.61	75.72
BS10(FR)C13/BS11(FR)C13	55.22	14.75	0.00	62.64
BS10C0(S1)	18.66	14.50	3.74	85.98
BS10C0(S1)	24.83	14.95	1.85	73.89
BS10(FR)C3(S1)	22.93	14.90	2.00	79.62
BS10(FR)C5(S1)	22.94	14.95	0.00	81.51
BS10(FR)C7(S1)	24.16	15.40	6.14	74.85
BS10(FR)C9(S1)	17.74	14.90	4.04	67.76
BS10(FR)C11(S1)	32.24	15.55	0.80	69.51
BS10(FR)C13(S1)	51.63	15.60	6.24	67.10
BS10(FR)C13(S1)	39.24	15.60	3.57	53.02
BS11C0(S1)	21.34	15.80	8.39	72.40
BS11C0(S1)	22.52	16.40	1.85	72.11
BS11(FR)C3(S1)	24.55	15.90	3.64	56.31
BS11(FR)C5(S1)	28.74	15.40	6.00	74.13
BS11(FR)C7(S1)	24.17	15.25	3.90	80.48
BS11(FR)C9(S1)	25.15	15.65	1.89	82.42
BS11(FR)C11(S1)	42.74	14.50	4.77	61.31
BS11(FR)C13(S1)	32.05	14.60	1.82	79.96
BS11(FR)C13(S1)	28.34	14.35	9.35	85.48

Appendix A5. (continued)

Population	YLD q ha ⁻¹	MST %	RL %	SL %
(BS10CO/BS11CO)(S1)	22.49	14.45	2.78	86.41
(BS10CO/BS11CO)(S1)	27.51	15.20	2.68	73.09
(BS10(FR)C3/BS11(FR)C3)(S1)	27.68	15.40	1.82	79.10
(BS10(FR)C5/BS11(FR)C5)(S1)	28.38	15.10	3.64	81.82
(BS10(FR)C7/BS11(FR)C7)(S1)	31.25	15.30	5.25	75.70
(BS10(FR)C9/BS11(FR)C9)(S1)	32.95	15.10	6.63	79.35
(BS10(FR)C11/BS11(FR)C11)(S1)	37.32	15.05	1.62	76.70
(BS10(FR)C13/BS11(FR)C13)(S1)	42.09	15.30	7.77	61.19
(BS10(FR)C13/BS11(FR)C13)(S1)	32.68	15.65	5.39	66.63
Mean of all entries	40.53	15.30	3.17	71.91
Standard error of an entry mean	5.41	0.35	2.02	6.79
LSD(0.05)	15.35	0.99	5.72	19.25

Appendix A6. Entry means at Fremont, Nebraska.

Population	YLD q ha ⁻¹	MST %	RL %	SL %
BS10C0	59.31	14.05	0.00	17.57
BS10C0	52.20	14.30	0.00	28.38
BS10(FR)C3	59.65	14.45	0.00	16.89
BS10(FR)C5	68.00	14.55	0.00	20.27
BS10(FR)C7	57.10	13.90	0.00	16.22
BS10(FR)C9	59.35	14.00	0.00	9.46
BS10(FR)C11	68.18	14.85	0.00	12.16
BS10(FR)C13	66.35	14.50	0.00	1.35
BS10(FR)C13	67.65	14.75	0.00	11.49
BS11C0	64.34	16.40	0.00	35.82
BS11C0	53.06	16.20	0.00	50.68
BS11(FR)C3	42.59	15.80	0.00	22.97
BS11(FR)C5	55.69	15.60	0.00	29.73
BS11(FR)C7	58.56	15.10	0.00	32.44
BS11(FR)C9	60.04	15.10	0.00	29.06
BS11(FR)C11	67.30	14.15	0.00	21.63
BS11(FR)C13	65.17	13.85	0.00	24.33
BS11(FR)C13	54.23	13.45	0.00	28.38
BS10C0/BS11C0	47.43	15.75	0.00	35.14
BS10C0/BS11C0	58.81	16.00	0.00	30.41
BS10(FR)C3/BS11(FR)C3	66.30	14.35	0.00	37.84
BS10(FR)C5/BS11(FR)C5	72.96	14.65	0.00	24.33
BS10(FR)C7/BS11(FR)C7	83.35	14.70	0.00	18.25
BS10(FR)C9/BS11(FR)C9	77.87	14.55	0.00	17.57
BS10(FR)C11/BS11(FR)C11	67.11	14.35	0.00	31.76
BS10(FR)C13/BS11(FR)C13	75.39	14.65	0.00	13.52
BS10(FR)C13/BS11(FR)C13	73.79	13.65	0.00	4.73
BS10C0(S1)	31.09	15.55	0.00	18.92
BS10C0(S1)	30.22	14.55	0.00	18.16
BS10(FR)C3(S1)	26.35	14.85	0.00	8.11
BS10(FR)C5(S1)	32.53	15.10	0.00	20.27
BS10(FR)C7(S1)	35.56	14.35	0.00	10.81
BS10(FR)C9(S1)	29.00	13.20	0.00	14.19
BS10(FR)C11(S1)	44.00	14.70	0.00	10.81
BS10(FR)C13(S1)	34.02	14.50	0.00	16.22
BS10(FR)C13(S1)	41.51	14.65	0.00	9.46
BS11C0(S1)	32.77	15.55	0.00	40.54
BS11C0(S1)	39.44	16.85	0.00	27.70
BS11(FR)C3(S1)	36.44	15.20	0.00	29.06
BS11(FR)C5(S1)	40.83	16.05	0.00	31.76
BS11(FR)C7(S1)	36.63	15.25	0.00	17.57
BS11(FR)C9(S1)	32.47	14.70	0.00	22.97
BS11(FR)C11(S1)	30.95	14.85	0.00	20.27
BS11(FR)C13(S1)	39.12	13.45	0.00	9.46
BS11(FR)C13(S1)	41.00	13.95	0.00	24.33

Appendix A6. (continued)

Population	YLD q ha ⁻¹	MST %	RL %	SL %
(BS10CO/BS11CO)(S1)	41.42	15.20	0.00	12.84
(BS10CO/BS11CO)(S1)	33.93	14.20	0.00	25.36
(BS10(FR)C3/BS11(FR)C3)(S1)	32.20	15.45	0.00	21.63
(BS10(FR)C5/BS11(FR)C5)(S1)	36.21	13.80	0.00	27.03
(BS10(FR)C7/BS11(FR)C7)(S1)	37.20	14.85	0.00	9.46
(BS10(FR)C9/BS11(FR)C9)(S1)	47.01	14.95	0.00	10.81
(BS10(FR)C11/BS11(FR)C11)(S1)	35.32	14.45	0.00	6.76
(BS10(FR)C13/BS11(FR)C13)(S1)	37.53	14.15	0.00	16.89
(BS10(FR)C13/BS11(FR)C13)(S1)	36.93	14.55	0.00	9.46
Mean of all entries	49.51	14.75	0.00	20.61
Standard error of an entry mean	5.99	0.39		7.32
LSD(0.05)	17.00	1.10		20.77

Appendix A7. Entry means at Crawfordsville, Iowa.

Population	YLD q ha ⁻¹	MST %
BS10C0	35.17	15.55
BS10C0	42.50	14.50
BS10(FR)C3	22.86	15.15
BS10(FR)C5	37.07	15.65
BS10(FR)C7	41.15	14.45
BS10(FR)C9	40.87	15.60
BS10(FR)C11	49.57	16.05
BS10(FR)C13	50.75	15.35
BS10(FR)C13	64.14	15.65
BS11C0	26.85	16.30
BS11C0	46.21	16.20
BS11(FR)C3	48.05	16.25
BS11(FR)C5	47.54	16.25
BS11(FR)C7	44.31	16.30
BS11(FR)C9	50.18	15.85
BS11(FR)C11	51.14	15.20
BS11(FR)C13	50.48	14.95
BS11(FR)C13	47.82	14.80
BS10C0/BS11C0	37.90	16.20
BS10C0/BS11C0	40.60	16.10
BS10(FR)C3/BS11(FR)C3	45.44	15.10
BS10(FR)C5/BS11(FR)C5	47.00	15.55
BS10(FR)C7/BS11(FR)C7	56.20	15.75
BS10(FR)C9/BS11(FR)C9	64.47	15.90
BS10(FR)C11/BS11(FR)C11	49.66	15.40
BS10(FR)C13/BS11(FR)C13	67.46	15.20
BS10(FR)C13/BS11(FR)C13	57.33	15.30
BS10C0(S1)	14.56	15.90
BS10C0(S1)	22.05	15.15
BS10(FR)C3(S1)	20.33	15.50
BS10(FR)C5(S1)	13.37	15.00
BS10(FR)C7(S1)	23.33	14.40
BS10(FR)C9(S1)	21.18	15.05
BS10(FR)C11(S1)	26.70	15.05
BS10(FR)C13(S1)	37.85	15.80
BS10(FR)C13(S1)	31.46	15.35
BS11C0(S1)	21.56	15.80
BS11C0(S1)	17.91	16.60
BS11(FR)C3(S1)	28.75	15.35
BS11(FR)C5(S1)	26.86	15.40
BS11(FR)C7(S1)	11.62	15.75
BS11(FR)C9(S1)	22.47	15.60
BS11(FR)C11(S1)	26.17	15.05
BS11(FR)C13(S1)	21.40	15.55
BS11(FR)C13(S1)	15.58	14.80

Appendix A7. (continued)

Population	YLD q ha ⁻¹	MST %
(BS10CO/BS11CO)(S1)	22.78	15.50
(BS10CO/BS11CO)(S1)	18.04	16.05
(BS10(FR)C3/BS11(FR)C3)(S1)	28.38	15.70
(BS10(FR)C5/BS11(FR)C5)(S1)	27.63	14.70
(BS10(FR)C7/BS11(FR)C7)(S1)	23.39	15.20
(BS10(FR)C9/BS11(FR)C9)(S1)	30.68	15.35
(BS10(FR)C11/BS11(FR)C11)(S1)	26.53	15.65
(BS10(FR)C13/BS11(FR)C13)(S1)	32.76	15.60
(BS10(FR)C13/BS11(FR)C13)(S1)	31.21	15.40
Mean of all entries	35.32	15.50
Standard error of an entry mean	5.02	0.32
LSD(0.05)	14.23	0.91

**APPENDIX B: EXPERIMENT TWO COMBINED ENTRY MEANS
ACROSS TWO ENVIRONMENTS FOR GRAIN YIELD (YLD),
GRAIN MOISTURE (MST), ROOT LODGING (RL), STALK
LODGING (SL), PLANT HEIGHT (PH), EAR HEIGHT (EH), AND
DAYS TO MID-ANTHESIS (DTA) AND MID-SILK (DTS)**

Appendix B1. Combined entry means at Ames and Ankeny, Iowa for BS10C0 S₁ lines.

Pedigree	YLD	MST	RL	SL	PH	EH	DTA	DTS
BS10C0)-01	31.70	18.00	0.00	25.70	205.00	107.25	82.25	86.25
BS10C0)-02	37.26	16.30	0.00	62.38	213.75	113.50	83.00	86.00
BS10C0)-03	45.89	16.63	2.98	31.59	202.75	95.75	83.00	86.25
BS10C0)-04	28.84	18.25	0.51	50.03	215.50	116.00	82.50	86.00
BS10C0)-05	38.04	15.35	1.50	26.73	195.75	108.75	81.25	84.25
BS10C0)-06	43.43	14.88	0.00	42.91	191.50	97.00	81.50	83.50
BS10C0)-07	38.80	17.15	0.52	28.88	239.75	135.25	84.00	85.50
BS10C0)-08	26.80	16.25	0.00	20.34	219.25	121.00	81.50	84.50
BS10C0)-09	27.37	20.15	0.49	27.53	225.00	120.00	86.25	91.25
BS10C0)-10	18.86	17.88	0.72	33.91	179.50	93.00	82.00	84.50
BS10C0)-11	29.42	14.18	0.00	28.25	192.25	95.00	81.00	83.00
BS10C0)-14	46.72	16.63	1.56	44.50	213.50	110.00	81.50	83.00
BS10C0)-15	39.17	15.00	0.00	33.59	189.75	103.25	81.00	83.00
BS10C0)-16	31.15	16.20	0.00	44.71	226.25	132.00	84.75	91.25
BS10C0)-17	33.45	15.43	0.00	51.32	219.50	123.00	82.50	86.25
BS10C0)-20	32.99	20.10	0.00	38.61	229.25	135.00	87.25	91.50
BS10C0)-21	34.43	15.53	1.07	51.23	211.75	109.00	83.25	85.00
BS10C0)-22	46.34	17.65	5.92	26.52	243.50	146.25	86.75	88.75
BS10C0)-24	36.94	14.98	0.52	66.28	192.00	102.00	80.00	80.25
BS10C0)-25	29.00	15.85	0.00	24.21	188.50	89.75	82.00	84.50
BS10C0)-27	33.02	15.80	0.53	59.96	180.50	103.50	83.00	84.25
BS10C0)-29	29.21	19.08	0.00	11.66	210.75	113.75	82.75	86.00
BS10C0)-30	32.29	16.25	0.00	50.44	201.75	111.25	82.50	85.00
BS10C0)-31	38.54	15.40	0.00	35.93	195.25	100.25	80.50	81.50
BS10C0)-34	35.84	15.48	0.00	28.00	193.75	100.25	81.00	84.00
BS10C0)-35	29.42	15.25	0.00	60.41	196.75	103.00	81.00	83.00
BS10C0)-37	25.27	20.18	0.00	45.36	165.25	90.25	82.75	85.50
BS10C0)-39	26.17	15.48	0.00	53.37	206.50	109.25	83.50	86.25
BS10C0)-40	24.64	18.68	0.00	32.40	225.25	119.75	87.50	93.25
BS10C0)-41	46.80	17.45	0.52	55.72	203.50	106.25	83.75	86.50
BS10C0)-42	39.54	15.03	0.00	21.36	198.75	101.25	80.50	82.50
BS10C0)-43	52.11	17.18	0.00	33.24	219.25	112.25	81.50	84.25
BS10C0)-46	31.33	17.18	0.56	37.16	190.00	101.00	80.50	82.50
BS10C0)-48	27.47	14.83	0.00	38.51	200.00	89.75	80.50	82.00
BS10C0)-49	21.79	14.85	1.14	59.62	181.00	101.00	83.50	85.75
BS10C0)-50	26.76	18.53	1.43	54.26	195.00	117.50	81.50	84.50
BS10C0)-51	34.93	17.58	0.00	45.63	218.00	118.00	80.50	82.00
BS10C0)-52	34.42	15.93	0.00	51.54	230.00	133.50	80.50	83.00
BS10C0)-53	44.02	17.65	0.00	52.71	193.00	89.00	81.00	82.50
BS10C0)-54	29.89	17.60	0.00	50.28	209.50	124.75	81.75	86.50
BS10C0)-56	30.25	17.05	0.00	31.03	181.50	82.00	82.00	84.75
BS10C0)-57	24.38	15.45	0.00	53.04	188.75	99.75	80.75	82.00
BS10C0)-58	34.24	18.63	1.02	35.06	220.50	117.75	83.75	87.25
BS10C0)-59	43.07	17.03	0.00	36.98	188.00	102.50	82.25	83.75
BS10C0)-60	40.19	15.78	0.00	54.79	206.25	116.25	81.50	83.25
BS10C0)-61	36.94	15.28	0.00	8.86	188.25	96.75	81.00	83.00

Appendix B1. (continued)

Pedigree	YLD	MST	RL	SL	PH	EH	DTA	DTS
BS10C0)-62	48.59	16.93	0.00	59.46	231.25	125.75	80.25	83.50
BS10C0)-63	28.44	18.15	0.00	47.57	192.25	108.25	83.00	85.00
BS10C0)-65	33.20	17.63	0.51	59.44	200.00	86.00	81.00	83.50
BS10C0)-67	33.50	14.73	0.56	15.89	215.25	120.00	82.25	83.75
BS10C0)-68	20.06	15.63	0.48	55.12	214.75	114.75	83.50	85.75
BS10C0)-69	41.03	15.18	0.00	68.31	213.25	111.00	80.50	82.00
BS10C0)-70	33.98	16.48	5.39	17.37	204.25	103.00	82.00	84.00
BS10C0)-71	39.35	14.80	0.00	25.47	217.25	123.75	81.75	85.00
BS10C0)-72	45.16	15.43	0.00	59.05	198.25	100.75	80.75	83.00
BS10C0)-73	19.83	14.95	2.33	59.21	166.75	89.50	80.75	81.75
BS10C0)-74	28.05	15.98	1.47	25.28	200.00	107.75	81.50	84.50
BS10C0)-75	31.93	16.68	0.00	53.17	214.50	111.00	80.75	84.00
BS10C0)-76	26.50	17.43	0.54	20.18	195.00	100.00	79.75	81.75
BS10C0)-77	41.47	15.93	1.50	52.28	220.00	111.00	80.25	83.00
BS10C0)-78	28.02	16.65	0.00	19.99	170.25	84.25	81.25	83.25
BS10C0)-79	37.92	17.03	0.00	54.69	199.25	108.25	82.25	87.00
BS10C0)-81	37.80	15.90	0.00	54.85	196.25	96.75	77.75	80.75
BS10C0)-82	24.97	16.70	0.00	38.42	196.75	103.00	83.50	87.00
BS10C0)-83	34.70	15.20	0.00	26.67	201.50	111.50	81.00	82.50
Means	33.90	16.53	0.52	41.06	203.50	108.15	82.03	84.62
SEM	3.78	0.41	1.05	8.98	4.87	4.36	0.60	0.91
LSD(0.05)	10.68	1.17	2.97	25.38	13.77	12.33	1.70	2.56

Appendix B2. Combined entry means at Ames and Ankeny, Iowa for BS10C13 S₁ lines.

Pedigree	YLD	MST	RL	SL	PH	EH	DTA	DTS
BS10(FR)C13)-01	56.72	15.25	0.00	54.47	215.25	113.25	80.50	82.50
BS10(FR)C13)-04	41.58	16.73	0.00	23.92	218.25	116.75	82.00	82.75
BS10(FR)C13)-05	47.31	16.58	0.00	22.45	200.50	106.50	80.50	84.00
BS10(FR)C13)-06	68.36	15.43	0.00	9.11	244.75	122.75	82.50	83.50
BS10(FR)C13)-07	42.49	18.00	0.00	7.09	225.00	119.25	82.50	85.00
BS10(FR)C13)-08	49.66	17.13	0.00	12.88	228.25	120.25	83.50	86.00
BS10(FR)C13)-09	41.75	19.25	0.50	4.26	223.00	119.50	82.50	84.00
BS10(FR)C13)-10	37.45	15.20	5.22	36.42	208.75	112.00	83.50	85.50
BS10(FR)C13)-11	37.63	17.73	1.09	15.34	217.25	118.25	83.00	84.75
BS10(FR)C13)-14	57.46	16.33	0.00	38.14	223.75	120.50	81.25	82.00
BS10(FR)C13)-16	32.21	17.30	0.00	31.43	194.25	93.75	80.25	81.50
BS10(FR)C13)-18	42.30	16.73	0.00	10.94	193.50	95.00	78.75	80.25
BS10(FR)C13)-19	49.10	18.00	0.00	15.64	202.25	95.75	81.50	82.50
BS10(FR)C13)-20	51.76	16.73	1.39	16.53	218.00	126.25	81.00	83.00
BS10(FR)C13)-21	33.23	15.88	1.07	14.13	211.25	92.25	80.75	82.50
BS10(FR)C13)-22	47.67	17.48	0.00	11.54	225.25	115.25	81.75	84.00
BS10(FR)C13)-23	48.30	14.85	0.98	42.01	221.00	114.00	83.00	85.00
BS10(FR)C13)-24	47.58	17.03	0.00	6.33	209.25	113.25	82.50	84.00
BS10(FR)C13)-26	35.94	16.60	0.00	4.04	187.00	87.00	80.75	82.50
BS10(FR)C13)-27	50.57	19.08	0.00	41.73	202.50	102.00	82.00	84.25
BS10(FR)C13)-28	57.64	17.30	0.00	11.64	217.50	114.75	80.75	82.50
BS10(FR)C13)-29	58.95	15.28	0.00	34.12	220.25	113.25	81.25	82.25
BS10(FR)C13)-30	58.23	16.38	0.00	36.80	226.75	124.25	82.50	84.00
BS10(FR)C13)-31	38.10	17.95	0.00	1.85	219.00	106.50	83.00	84.75
BS10(FR)C13)-32	57.01	15.98	0.50	26.23	216.25	112.00	81.50	81.75
BS10(FR)C13)-33	46.55	17.13	0.00	18.13	214.25	112.75	80.25	81.50
BS10(FR)C13)-34	30.77	17.08	0.00	8.88	188.75	96.25	81.75	82.50
BS10(FR)C13)-35	55.00	16.88	0.00	7.08	207.50	106.75	80.75	82.00
BS10(FR)C13)-36	32.60	15.03	1.05	48.64	206.50	104.25	81.00	82.50
BS10(FR)C13)-37	55.26	15.33	0.00	47.62	219.25	120.75	80.50	81.25
BS10(FR)C13)-38	46.70	16.40	0.00	30.43	210.25	110.25	80.50	81.75
BS10(FR)C13)-39	47.89	16.95	0.00	17.14	199.25	109.50	80.75	82.50
BS10(FR)C13)-40	53.55	17.25	0.56	18.61	222.50	119.50	82.50	84.00
BS10(FR)C13)-41	29.88	15.38	0.54	31.66	214.25	119.50	83.50	86.00
BS10(FR)C13)-42	41.03	16.58	1.53	17.24	234.75	125.00	85.75	86.75
BS10(FR)C13)-43	46.94	15.50	1.42	49.31	210.25	112.50	81.00	82.50
BS10(FR)C13)-45	60.78	17.53	0.00	9.74	225.25	113.75	81.25	82.50
BS10(FR)C13)-46	33.86	14.95	0.51	11.21	194.00	98.25	78.75	80.75
BS10(FR)C13)-48	41.21	15.13	0.00	19.33	208.50	114.50	80.50	81.00
BS10(FR)C13)-49	35.39	16.28	0.47	34.71	219.50	111.50	80.00	81.50
BS10(FR)C13)-50	49.29	18.68	0.00	7.00	201.00	98.50	82.50	83.75
BS10(FR)C13)-52	53.01	15.33	0.00	27.07	230.00	128.50	82.50	83.00
BS10(FR)C13)-53	36.13	16.08	0.00	10.41	216.25	110.25	82.50	85.50
BS10(FR)C13)-54	47.33	16.18	0.00	53.69	225.75	121.00	80.50	82.00
BS10(FR)C13)-56	44.22	15.73	0.00	22.70	217.25	106.50	79.75	80.25
BS10(FR)C13)-57	36.61	19.03	0.00	3.13	222.00	111.00	81.75	85.75

Appendix B2. (continued)

Pedigree	YLD	MST	RL	SL	PH	EH	DTA	DTS
BS10(FR)C13)-59	50.48	15.85	0.00	8.32	220.25	112.50	82.50	84.00
BS10(FR)C13)-60	34.43	16.90	0.50	13.37	224.00	122.50	83.50	84.25
BS10(FR)C13)-61	52.45	15.80	0.00	35.43	221.00	114.25	79.75	80.50
BS10(FR)C13)-62	34.89	18.23	3.36	3.45	231.00	117.75	85.75	87.00
BS10(FR)C13)-65	59.12	17.33	0.49	18.60	221.25	112.00	82.00	83.00
BS10(FR)C13)-66	44.61	17.68	0.00	8.81	209.25	112.25	80.75	81.00
BS10(FR)C13)-68	42.72	16.48	0.00	7.13	210.50	112.25	81.50	83.75
BS10(FR)C13)-69	25.97	15.40	0.00	14.29	196.25	102.50	83.50	85.00
BS10(FR)C13)-71	61.68	17.45	1.44	8.36	231.25	131.25	82.00	84.00
BS10(FR)C13)-72	41.40	15.68	0.00	50.21	213.25	114.50	79.25	79.50
BS10(FR)C13)-73	35.02	16.68	0.00	3.49	221.50	118.75	83.00	87.00
BS10(FR)C13)-76	48.34	15.60	0.48	42.86	232.50	123.25	82.00	82.50
BS10(FR)C13)-77	49.75	15.98	0.00	19.07	223.75	125.25	82.50	84.00
BS10(FR)C13)-79	56.89	15.80	0.52	5.87	232.75	115.50	83.00	84.50
BS10(FR)C13)-80	44.27	16.55	0.00	21.98	227.25	120.25	85.25	85.75
BS10(FR)C13)-82	36.82	16.90	0.00	4.39	216.00	118.00	82.50	84.25
BS10(FR)C13)-84	41.60	16.55	0.49	10.84	204.25	100.25	79.75	81.50
BS10(FR)C13)-85	48.11	18.50	0.00	7.57	227.25	114.75	83.00	85.75
BS10(FR)C13)-86	36.57	15.83	0.64	15.29	228.50	118.75	81.00	82.50
Means	45.51	16.61	0.38	20.34	216.12	112.79	81.75	83.29
SEM	4.48	0.42	0.77	10.35	4.93	3.25	0.73	0.96
LSD(0.05)	12.67	1.17	2.17	29.23	13.92	9.17	2.07	2.72

Appendix B3. Combined entry means at Ames and Ankeny, Iowa for BS11C0 S₁ lines.

Pedigree	YLD	MST	RL	SL	PH	EH	DTA	DTS
BS11C0)-01	28.88	19.28	0.00	31.10	236.50	132.25	86.50	90.00
BS11C0)-02	20.85	19.03	0.50	8.79	205.25	103.75	83.00	88.50
BS11C0)-03	23.94	16.50	0.51	62.78	206.25	114.75	81.75	85.25
BS11C0)-04	21.68	23.03	0.00	14.18	218.25	123.75	90.50	93.50
BS11C0)-05	21.58	17.73	0.00	39.09	245.75	144.00	86.50	89.75
BS11C0)-06	37.14	17.90	0.00	47.81	204.00	116.25	83.00	83.50
BS11C0)-07	30.64	18.53	1.04	28.58	224.50	126.25	87.25	89.25
BS11C0)-08	9.01	17.63	0.00	95.23	200.75	105.50	82.25	87.75
BS11C0)-09	32.11	20.23	1.74	25.10	221.00	121.75	82.50	86.75
BS11C0)-10	37.04	18.93	0.94	24.72	220.25	121.00	83.00	86.50
BS11C0)-11	19.44	18.75	2.43	77.10	207.25	119.50	86.00	92.25
BS11C0)-12	38.98	21.38	0.52	23.21	227.75	115.00	85.00	89.25
BS11C0)-13	29.73	17.78	0.00	32.37	214.25	104.00	83.50	86.25
BS11C0)-14	20.05	17.15	0.00	61.52	215.25	128.25	85.00	90.25
BS11C0)-15	28.32	17.98	4.36	35.62	234.00	123.50	82.75	89.25
BS11C0)-16	33.58	23.35	0.96	33.44	229.75	132.00	87.00	90.50
BS11C0)-17	24.48	18.53	0.93	36.62	224.25	130.75	83.50	87.25
BS11C0)-18	44.20	17.98	0.96	47.35	225.75	132.50	86.00	87.75
BS11C0)-20	34.53	20.58	0.00	51.09	197.50	108.25	83.00	87.00
BS11C0)-21	36.05	16.45	1.47	61.80	241.75	151.25	84.00	86.75
BS11C0)-22	21.97	17.50	0.61	60.10	200.25	107.00	81.25	84.50
BS11C0)-24	13.54	24.30	28.04	3.25	225.00	123.50	89.00	93.50
BS11C0)-25	36.06	16.38	0.00	36.70	205.25	111.75	82.75	86.50
BS11C0)-26	42.50	19.00	1.21	40.30	214.00	115.50	81.50	83.50
BS11C0)-27	23.53	19.43	0.54	26.07	222.50	137.50	87.00	90.00
BS11C0)-29	36.98	17.55	0.56	53.32	190.75	110.75	84.00	87.25
BS11C0)-30	23.60	15.43	0.00	63.33	224.25	141.00	84.50	89.75
BS11C0)-31	29.83	17.08	1.42	44.18	209.00	99.00	82.00	86.50
BS11C0)-32	20.93	18.45	1.48	59.31	226.25	135.75	88.75	91.50
BS11C0)-33	13.70	16.55	2.20	54.71	219.50	129.25	86.75	88.50
BS11C0)-34	22.33	18.15	1.00	49.07	210.00	123.00	85.25	88.50
BS11C0)-35	39.11	16.10	0.00	61.85	245.50	147.25	83.50	86.25
BS11C0)-39	28.08	19.70	0.00	38.60	241.75	147.25	87.25	92.00
BS11C0)-40	26.31	21.60	0.54	9.36	219.25	123.00	86.75	91.75
BS11C0)-41	42.94	16.40	0.00	50.63	228.25	138.00	83.50	87.00
BS11C0)-42	30.59	16.25	4.72	55.85	209.25	118.25	81.25	84.00
BS11C0)-43	25.03	19.03	4.24	32.59	226.75	132.00	86.75	89.50
BS11C0)-44	30.37	15.93	2.72	33.38	222.00	122.75	84.50	89.00
BS11C0)-45	34.44	18.60	3.26	29.91	200.75	117.50	83.50	87.50
BS11C0)-47	34.75	20.15	1.02	6.06	236.25	114.75	84.00	86.25
BS11C0)-48	26.77	19.20	0.54	22.89	199.50	112.00	86.25	89.00
BS11C0)-51	41.68	19.25	1.09	12.12	207.75	112.25	83.50	84.75
Means	28.98	18.59	1.70	40.02	218.66	123.17	84.65	88.20
SEM	3.53	0.56	3.15	9.72	4.41	3.87	0.86	1.11
LSD(0.05)	10.08	1.60	8.99	27.75	12.59	11.05	2.45	3.16

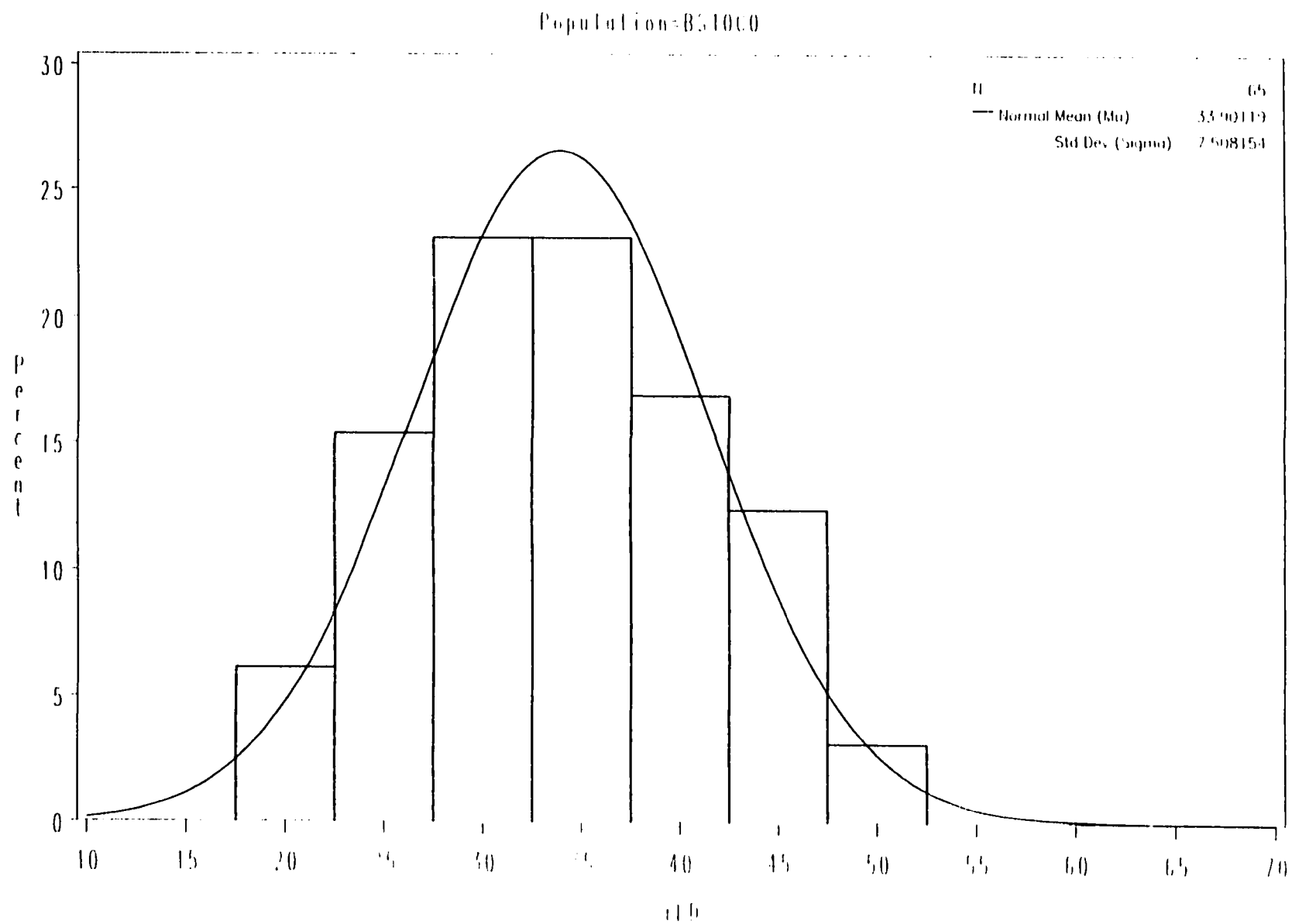
Appendix B4. Combined entry means at Ames and Ankeny, Iowa for BS11C13 S₁ lines.

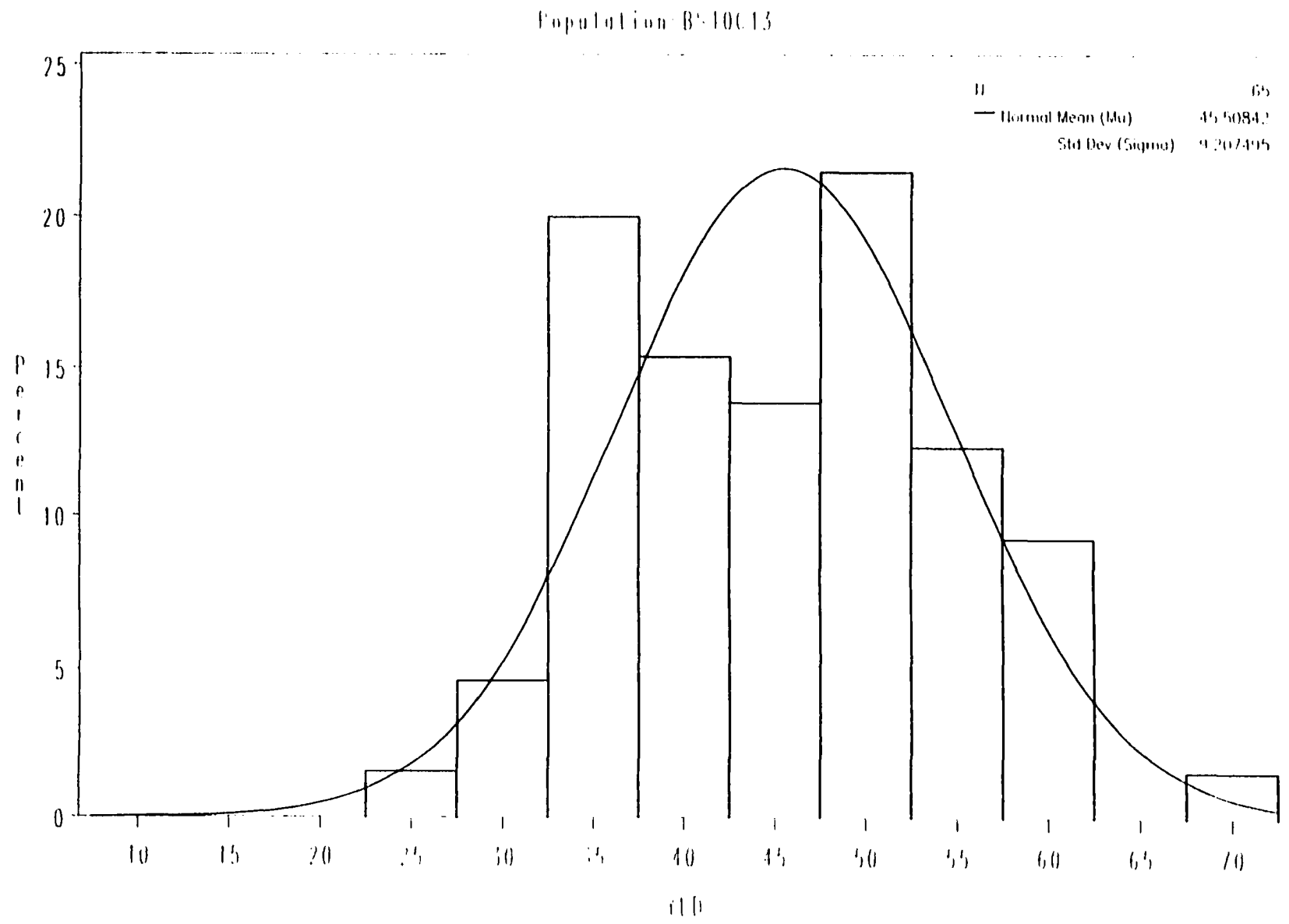
Pedigree	YLD	MST	RL	SL	PH	EH	DTA	DTS
BS11(FR)C13)-02	49.74	16.05	0.00	18.87	209.00	109.25	83.25	85.25
BS11(FR)C13)-04	46.80	15.95	1.98	6.96	212.50	91.25	79.00	83.00
BS11(FR)C13)-05	37.44	14.48	0.50	25.25	214.00	101.75	80.25	82.50
BS11(FR)C13)-06	44.39	15.33	0.00	21.64	210.00	106.25	82.25	83.50
BS11(FR)C13)-08	29.75	16.38	4.83	47.00	234.75	112.50	80.75	84.00
BS11(FR)C13)-09	38.80	17.38	0.49	16.30	246.25	130.50	84.50	87.25
BS11(FR)C13)-12	55.77	14.70	0.51	16.63	231.25	131.00	84.25	85.50
BS11(FR)C13)-13	55.32	16.30	0.00	9.43	248.50	124.50	83.50	85.25
BS11(FR)C13)-14	30.15	15.00	0.52	43.16	206.75	91.00	80.50	84.00
BS11(FR)C13)-15	35.78	14.90	2.05	46.78	217.25	108.00	81.25	82.75
BS11(FR)C13)-16	35.29	14.85	0.00	37.48	211.25	104.25	80.50	83.00
BS11(FR)C13)-17	39.68	16.98	0.00	2.21	209.25	111.00	83.25	83.75
BS11(FR)C13)-18	28.16	15.63	0.00	17.65	246.50	123.50	83.00	86.50
BS11(FR)C13)-19	57.48	15.78	0.00	19.69	246.50	130.00	82.50	83.50
BS11(FR)C13)-20	40.71	14.58	0.00	31.79	199.75	96.75	78.75	82.50
BS11(FR)C13)-21	44.12	15.75	0.00	16.03	215.75	104.50	80.50	83.00
BS11(FR)C13)-22	45.87	14.63	0.51	55.70	195.25	109.00	81.75	84.25
BS11(FR)C13)-23	30.54	15.38	0.00	35.45	187.75	98.75	81.75	84.00
BS11(FR)C13)-24	44.21	15.80	1.96	33.01	218.75	98.00	81.50	84.00
BS11(FR)C13)-25	33.54	15.98	1.67	6.56	215.50	87.50	81.50	84.00
BS11(FR)C13)-28	47.99	15.08	0.50	52.54	225.25	115.00	82.75	84.50
BS11(FR)C13)-29	15.63	15.13	4.00	42.96	238.00	118.25	83.00	87.00
BS11(FR)C13)-30	36.56	15.75	0.54	38.00	234.50	119.25	80.50	84.00
BS11(FR)C13)-31	29.36	15.13	0.00	29.04	230.75	110.00	85.50	89.25
BS11(FR)C13)-33	50.02	14.63	1.09	35.22	204.50	113.50	81.75	83.50
BS11(FR)C13)-34	30.79	14.70	0.00	66.74	242.25	124.75	84.75	85.25
BS11(FR)C13)-35	34.81	15.20	0.00	33.89	227.50	128.50	81.25	82.50
BS11(FR)C13)-36	28.94	14.48	0.00	30.58	244.25	124.25	83.00	85.00
BS11(FR)C13)-37	45.02	14.48	0.99	38.03	219.50	116.75	80.50	81.50
BS11(FR)C13)-38	31.57	14.48	0.00	39.06	223.25	108.50	84.25	87.00
BS11(FR)C13)-39	54.29	15.58	1.04	16.74	225.50	115.00	84.00	85.25
BS11(FR)C13)-41	40.61	16.13	2.55	9.82	235.25	128.75	84.50	87.25
BS11(FR)C13)-42	23.32	14.95	3.41	36.82	226.50	117.75	86.75	89.50
BS11(FR)C13)-43	38.55	14.75	1.62	41.80	173.50	90.50	79.00	81.50
BS11(FR)C13)-45	34.02	14.30	3.55	28.53	238.25	112.50	82.50	85.00
BS11(FR)C13)-46	53.98	15.03	1.03	34.68	209.50	117.50	81.25	84.00
BS11(FR)C13)-47	37.38	14.98	0.53	61.17	226.50	116.50	82.00	84.00
BS11(FR)C13)-48	35.72	15.60	0.00	50.13	220.75	106.75	79.00	81.00
BS11(FR)C13)-49	46.11	15.60	0.00	45.50	226.25	120.00	81.75	84.00
BS11(FR)C13)-50	38.07	14.95	0.98	22.48	228.50	97.50	82.50	84.25
BS11(FR)C13)-51	41.06	14.50	0.00	7.56	211.00	103.00	77.75	82.00
BS11(FR)C13)-52	37.27	15.40	0.00	27.46	218.50	107.50	82.75	83.25
BS11(FR)C13)-53	45.59	15.53	0.00	41.45	227.25	111.00	81.00	82.00
BS11(FR)C13)-54	35.63	16.00	0.00	25.48	212.25	92.25	80.50	85.50
BS11(FR)C13)-55	28.91	15.08	0.00	40.19	215.50	109.50	82.50	84.00
BS11(FR)C13)-56	21.88	15.73	0.00	22.66	208.50	96.00	82.50	87.25

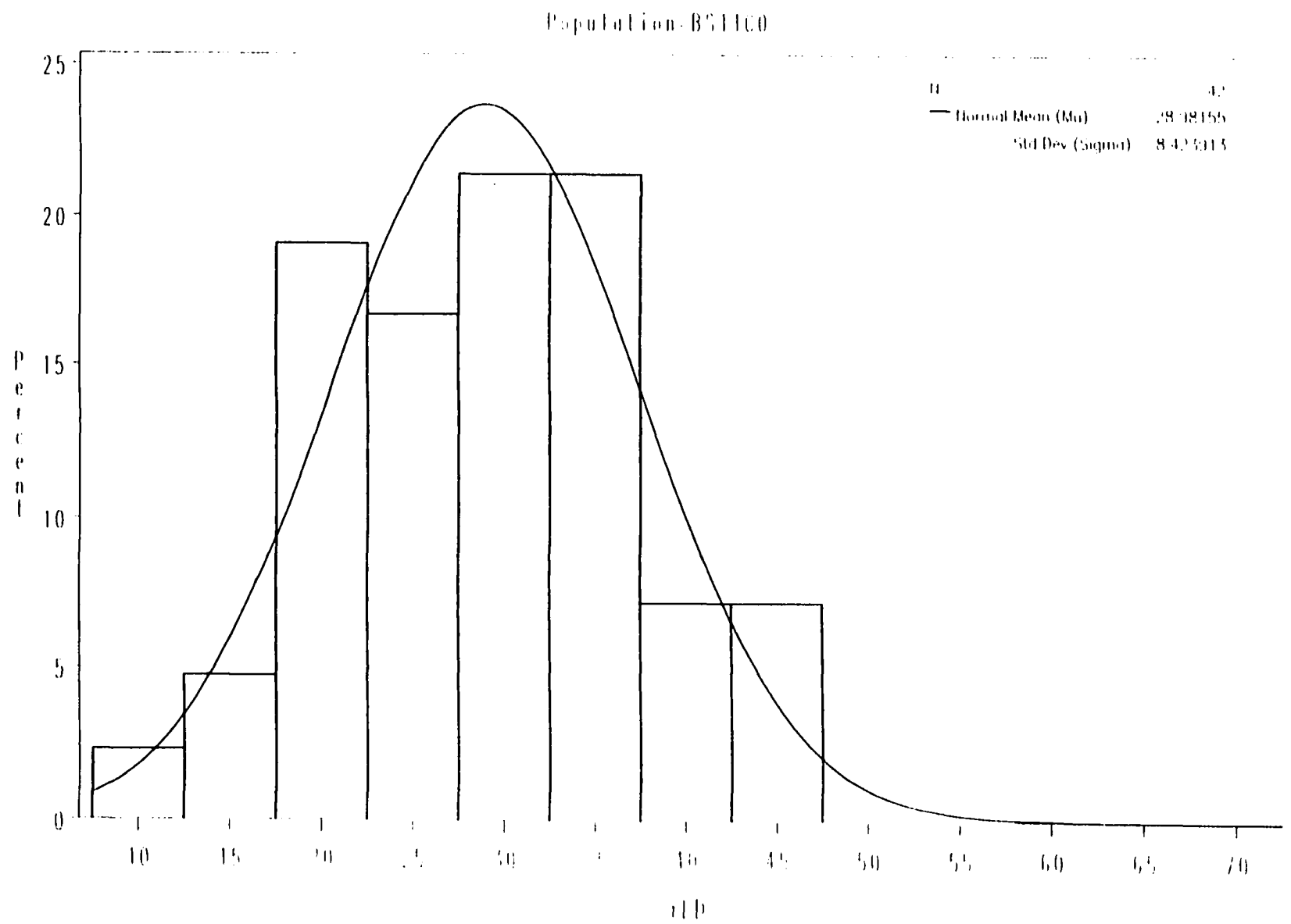
Appendix B4. (continued)

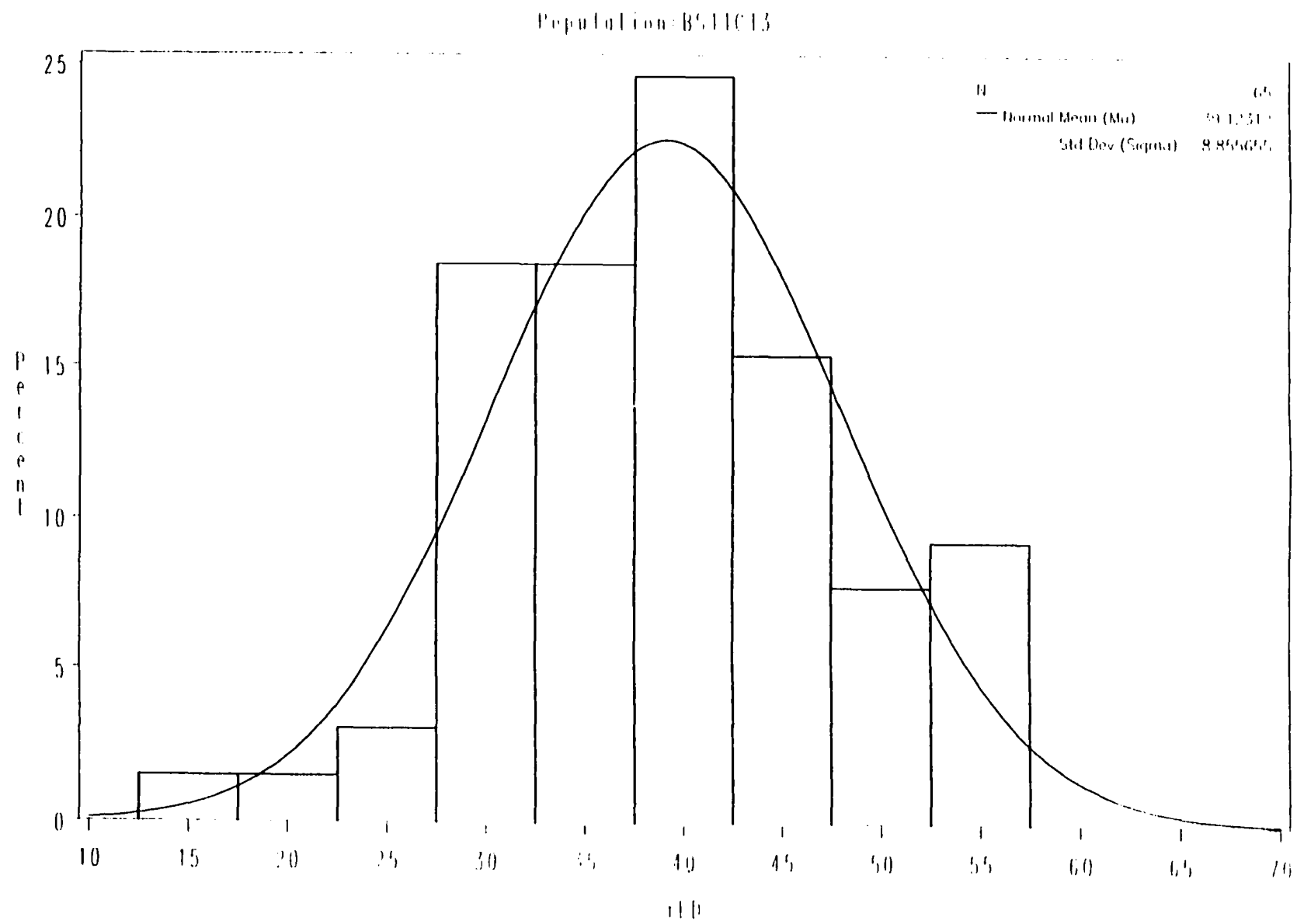
Pedigree	YLD	MST	RL	SL	PH	EH	DTA	DTS
BS11(FR)C13)-58	44.02	15.63	0.00	21.53	216.50	99.50	81.00	82.75
BS11(FR)C13)-59	50.39	16.08	0.00	6.59	218.75	100.25	82.00	83.25
BS11(FR)C13)-60	39.56	14.35	0.50	16.61	226.25	108.75	81.25	83.00
BS11(FR)C13)-61	57.21	16.45	0.00	8.65	233.25	105.75	82.50	85.25
BS11(FR)C13)-62	45.11	15.13	1.56	45.95	237.25	121.75	82.75	84.00
BS11(FR)C13)-63	34.93	16.45	0.00	11.45	225.50	114.00	83.50	85.75
BS11(FR)C13)-64	39.91	15.90	0.64	11.55	223.25	109.25	81.00	84.00
BS11(FR)C13)-65	38.52	15.10	0.96	59.14	228.00	114.25	80.50	82.00
BS11(FR)C13)-66	38.70	12.90	1.00	34.22	213.50	110.00	79.75	83.00
BS11(FR)C13)-68	39.93	16.18	0.54	11.20	235.75	111.00	83.50	86.00
BS11(FR)C13)-69	41.17	15.68	0.00	61.68	226.25	111.75	81.00	82.75
BS11(FR)C13)-73	25.72	14.70	6.44	54.98	219.00	106.50	80.50	82.00
BS11(FR)C13)-74	40.00	16.38	0.00	10.98	227.50	118.00	84.00	85.25
BS11(FR)C13)-75	28.61	14.85	0.00	57.55	231.00	125.75	83.25	84.75
BS11(FR)C13)-77	40.68	16.10	2.01	8.00	254.25	121.50	82.75	84.00
BS11(FR)C13)-78	41.63	18.50	0.50	6.02	226.75	103.25	82.00	88.00
BS11(FR)C13)-80	47.66	14.88	0.97	19.75	223.00	112.75	81.00	84.50
BS11(FR)C13)-86	31.54	14.30	3.52	59.98	204.75	96.75	80.25	82.75
BS11(FR)C13)-90	31.20	15.28	2.04	51.60	230.25	113.75	84.25	85.25
Means	39.12	15.38	0.89	30.52	222.62	110.68	81.98	84.29
SEM	4.26	0.36	1.31	9.69	3.90	3.39	0.63	0.71
LSD(0.05)	12.03	1.03	3.71	27.39	11.03	9.58	1.79	2.01

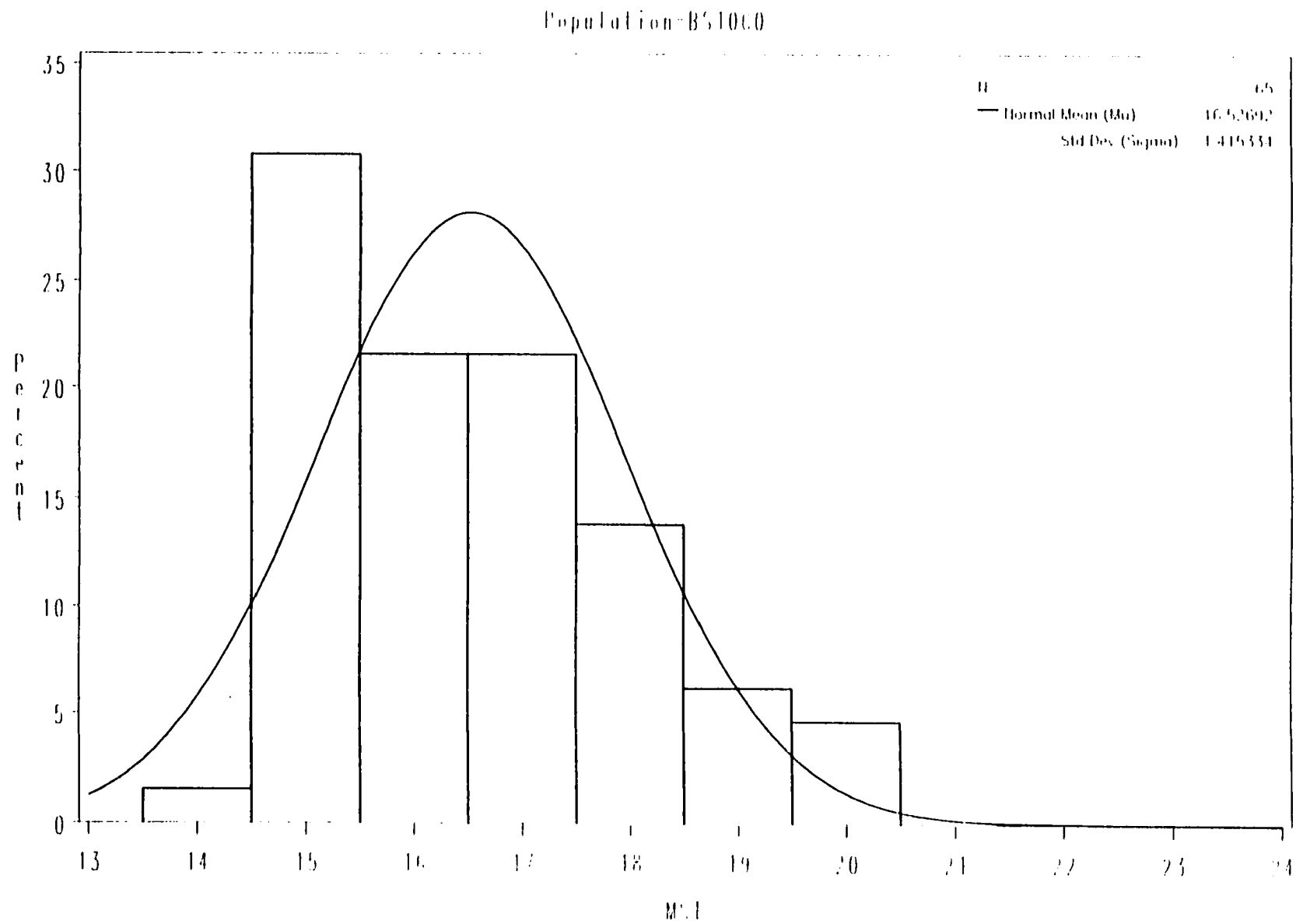
**APPENDIX C: HISTOGRAMS AND NORMALITY DISTRIBUTIONS
FOR EXPERIMENT TWO RANDOM S₁ LINE MEANS COMBINED
ACROSS TWO ENVIRONMENTS**

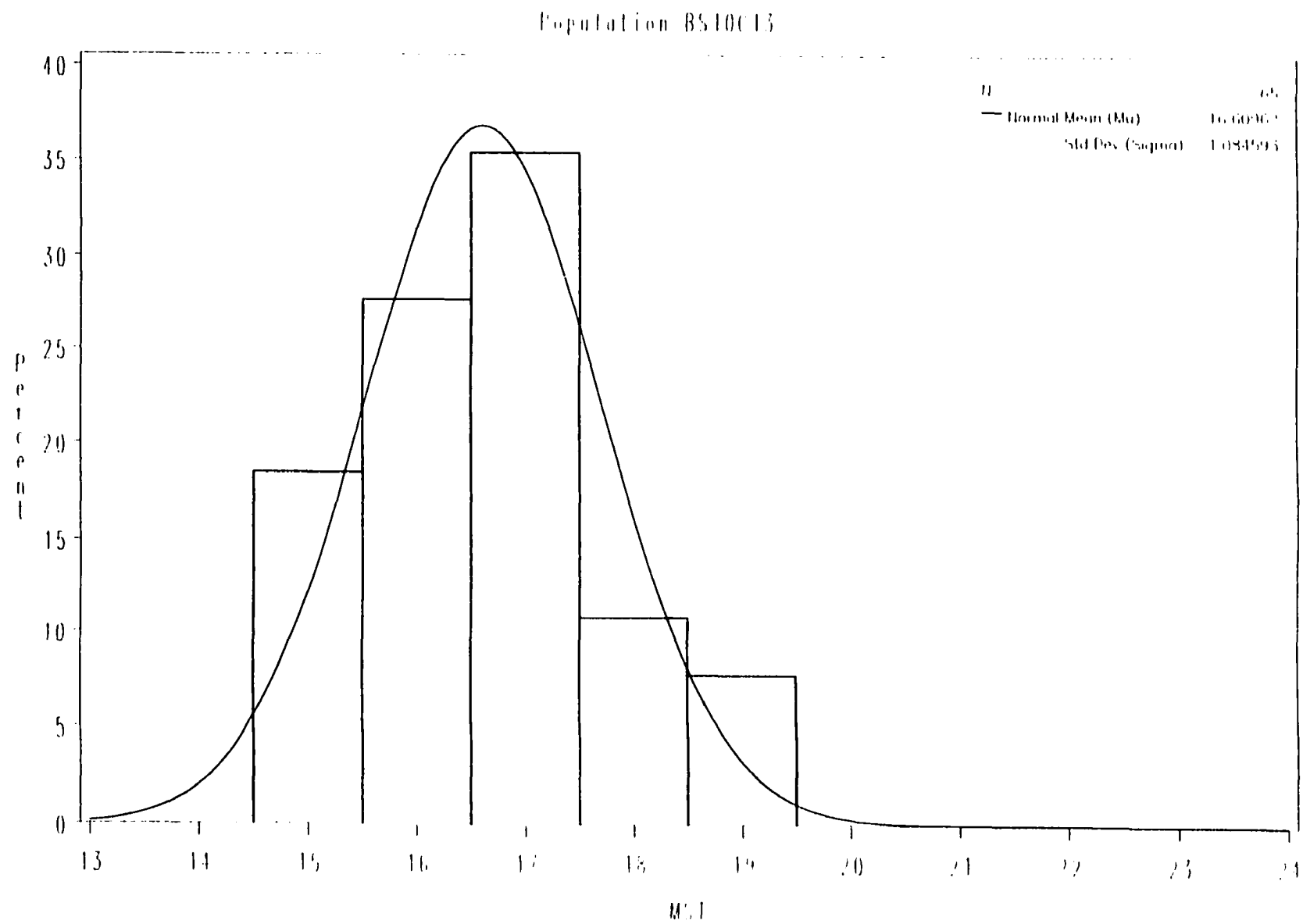


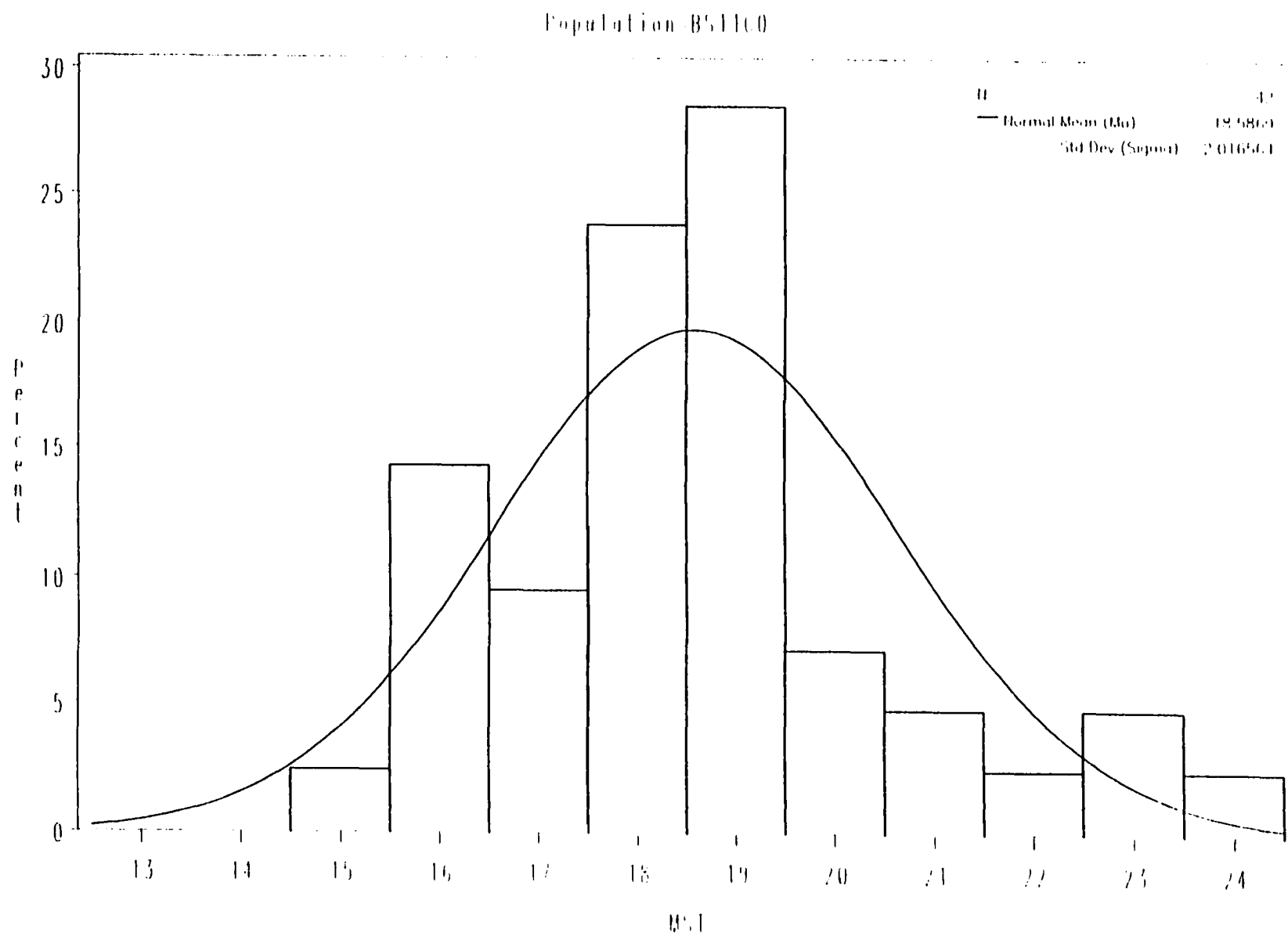


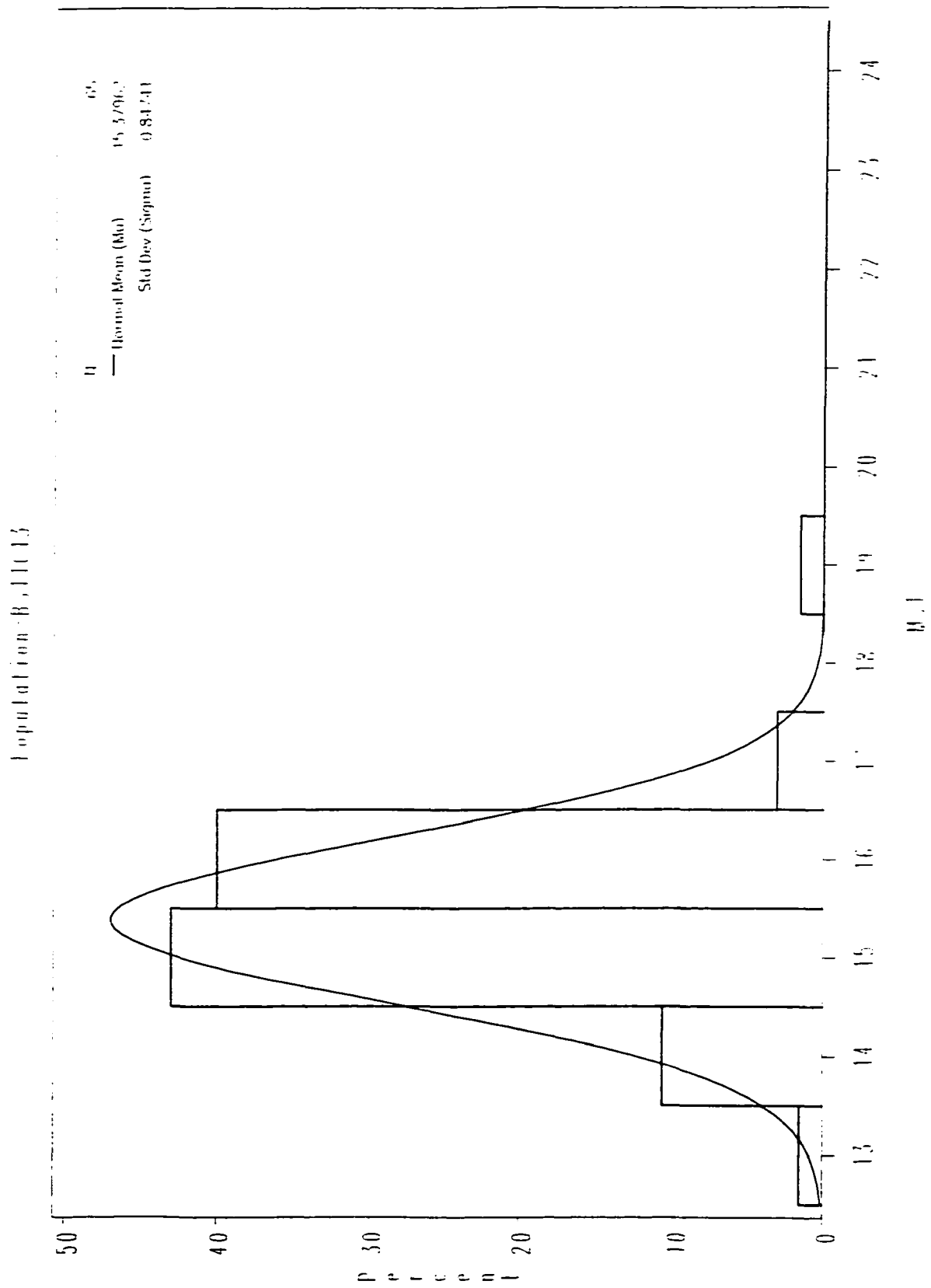




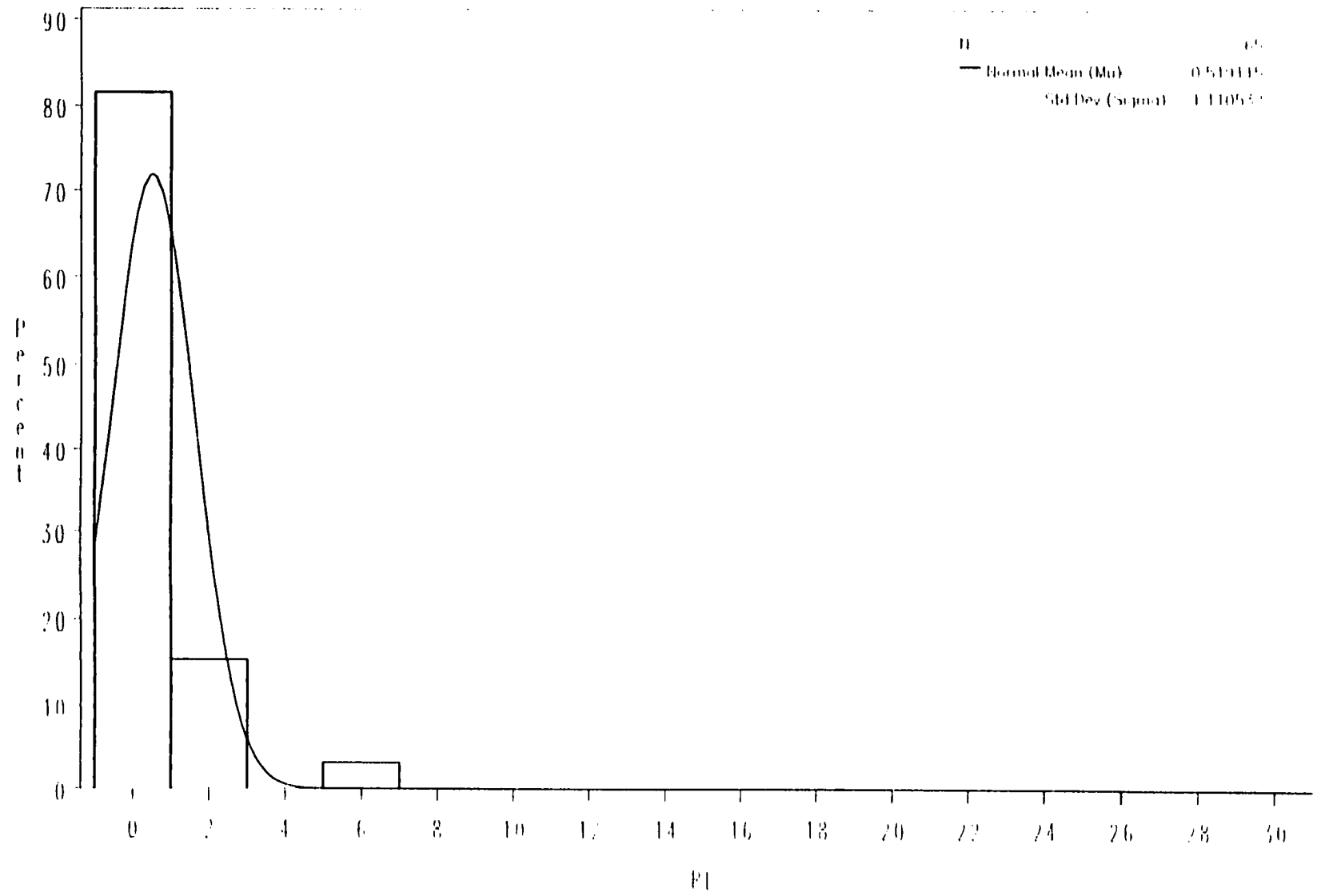




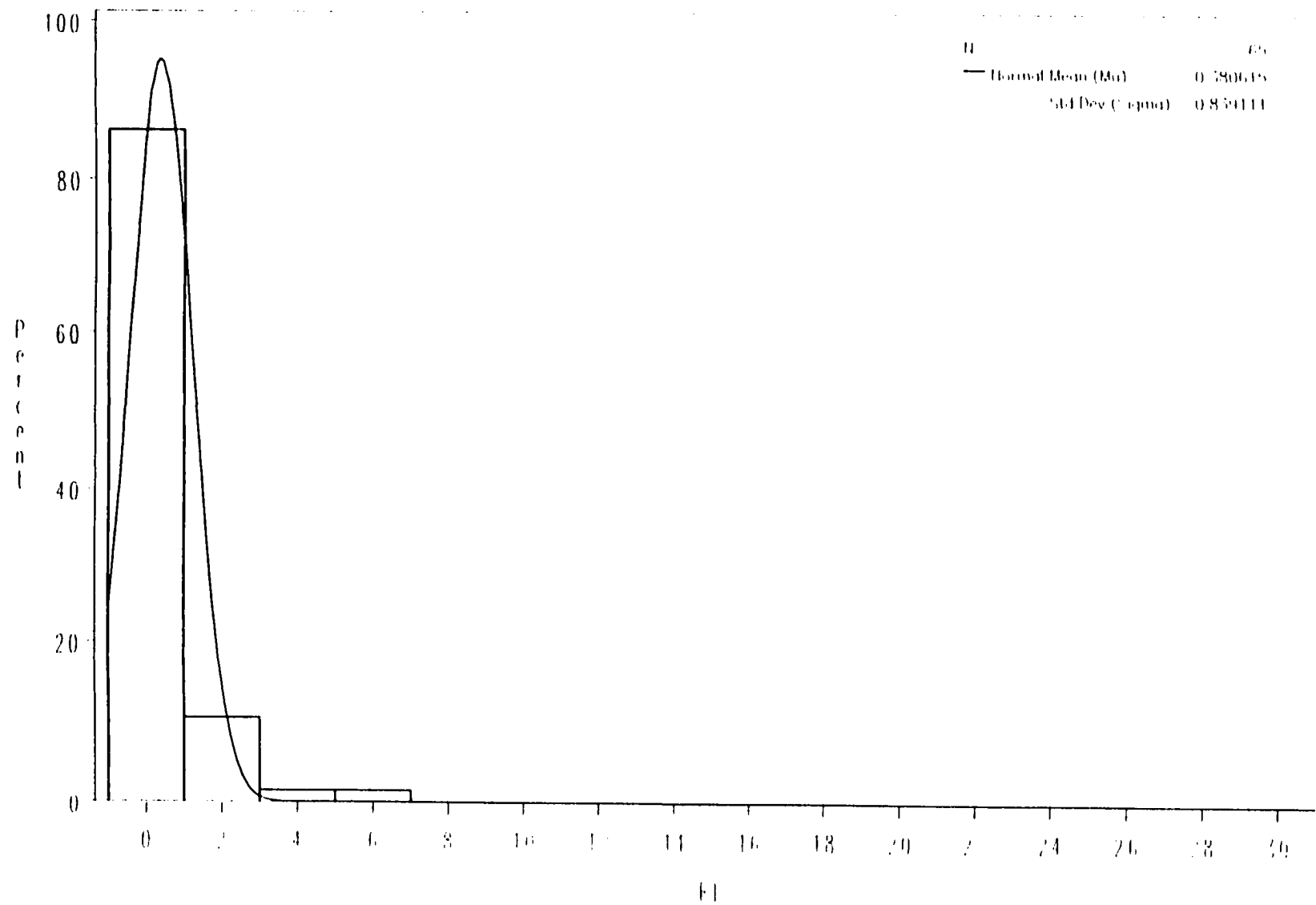




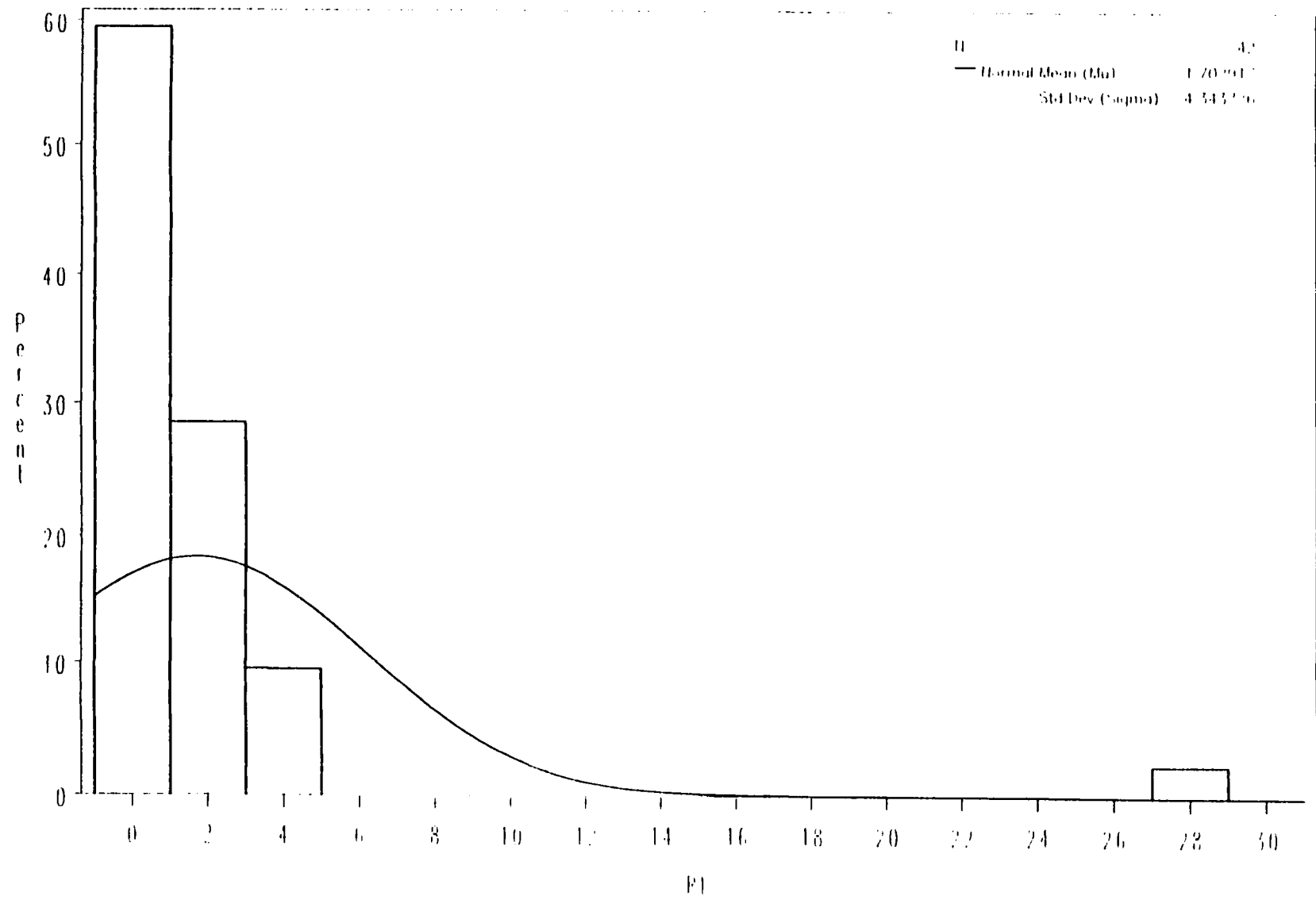
Population BS10C0



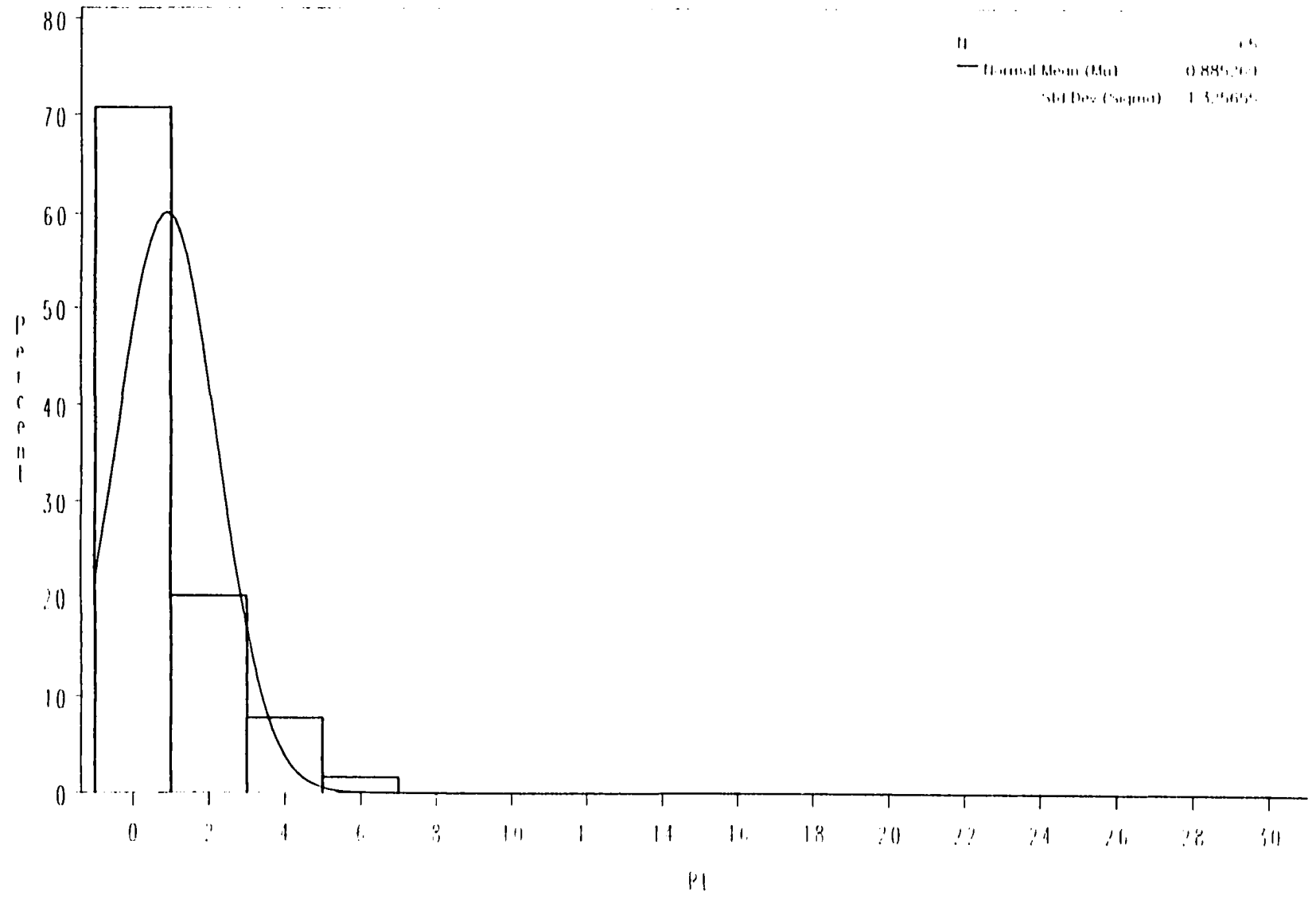
Population: 8510013

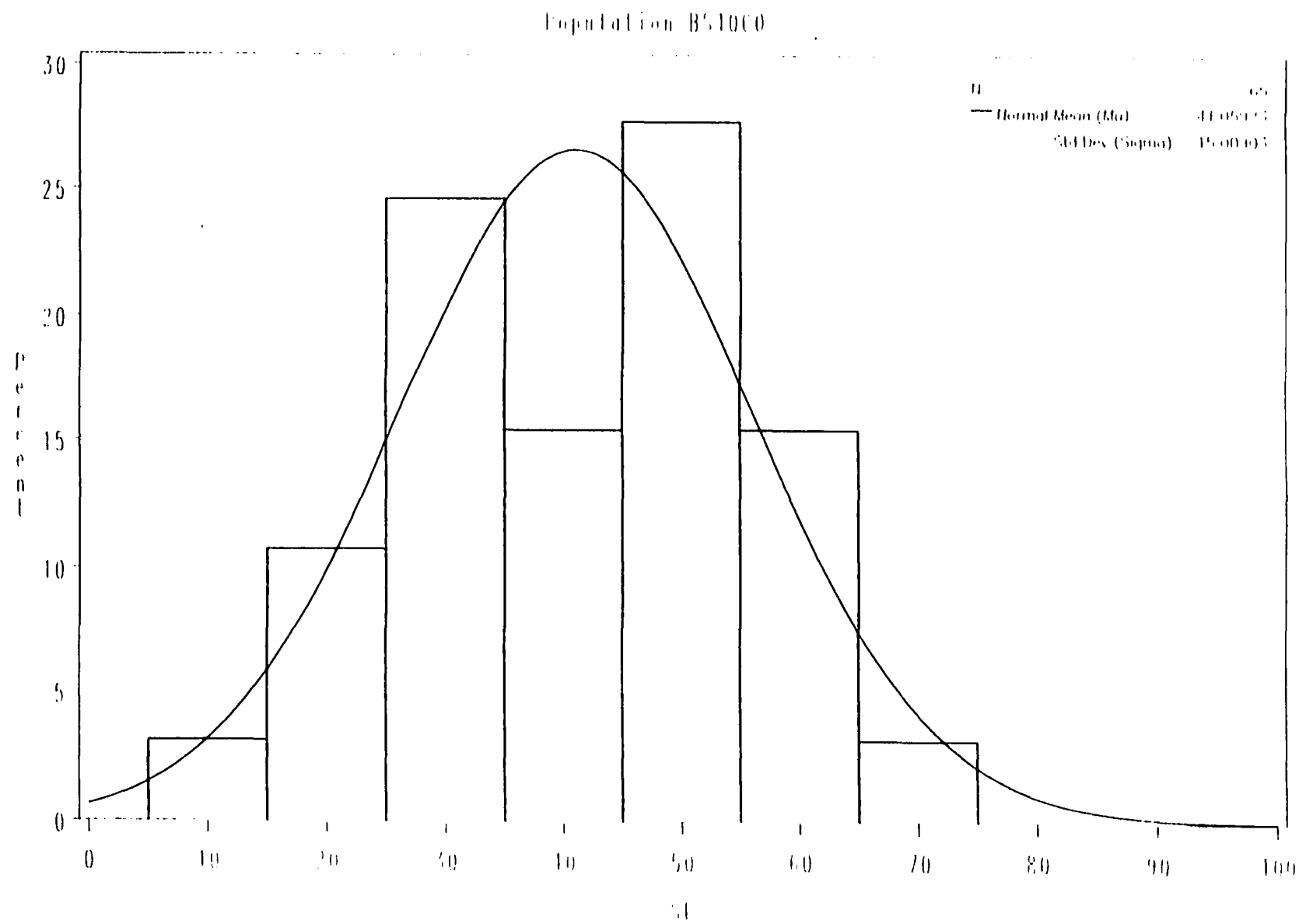


Population B51.10.0

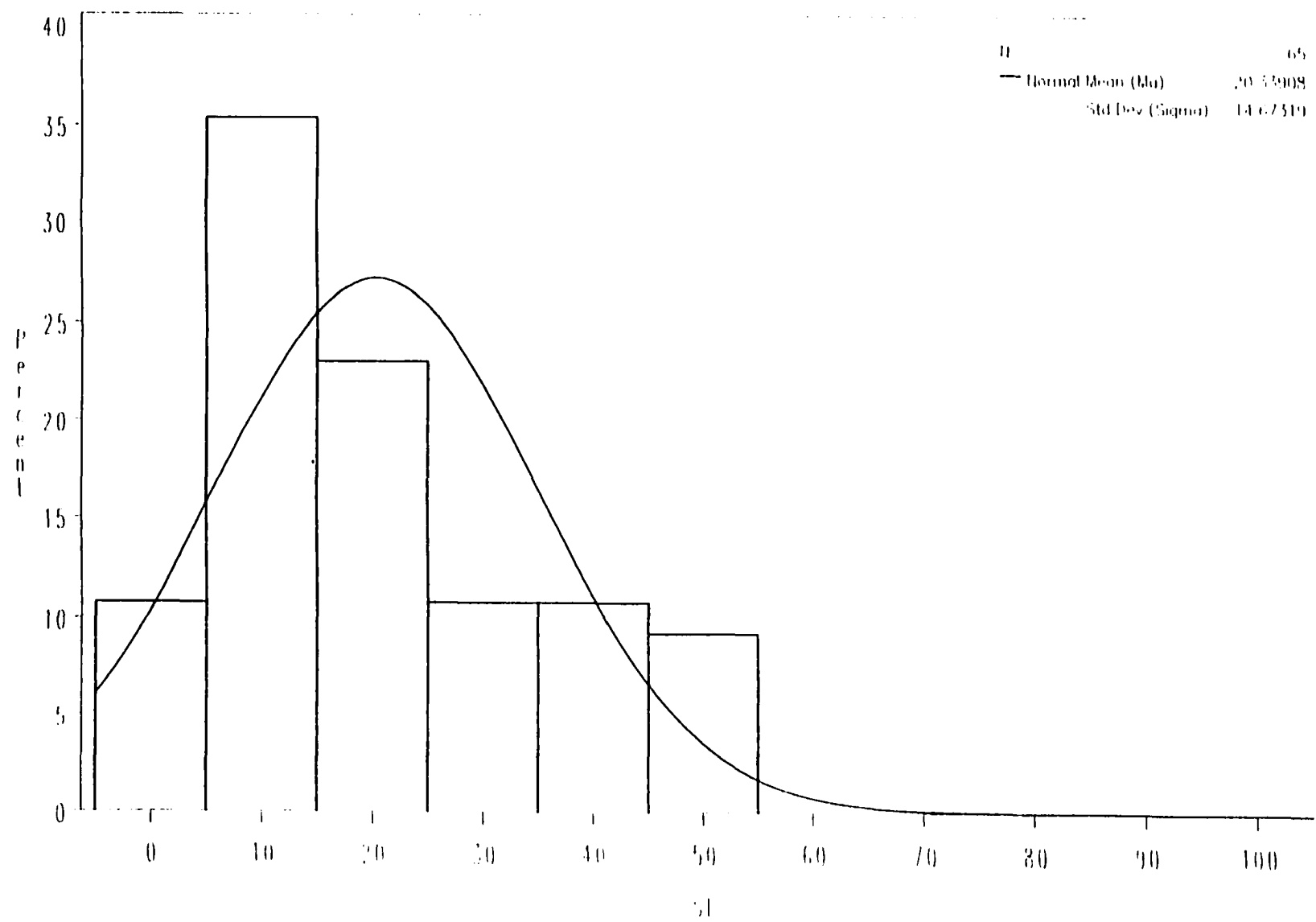


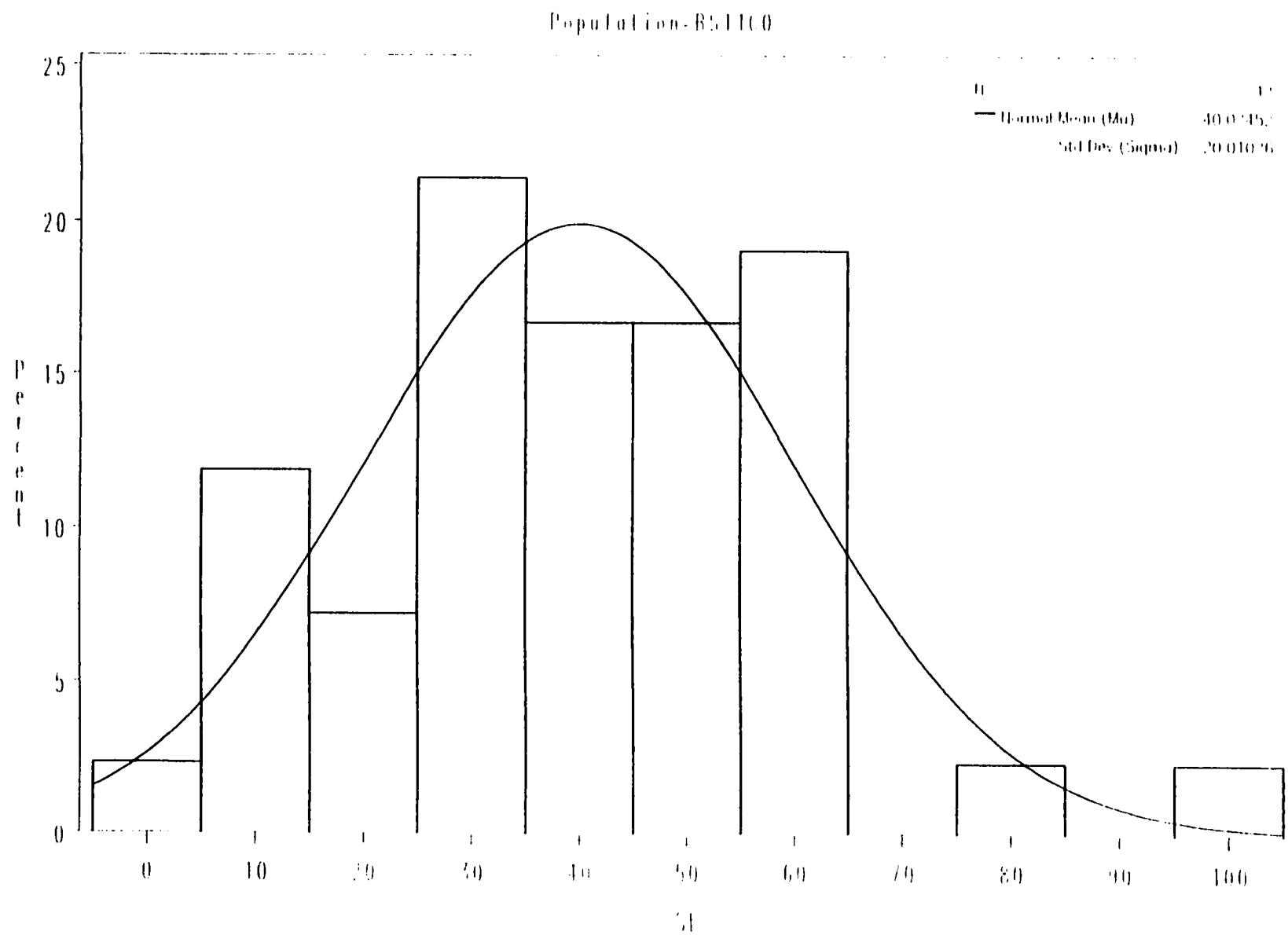
Population B11013

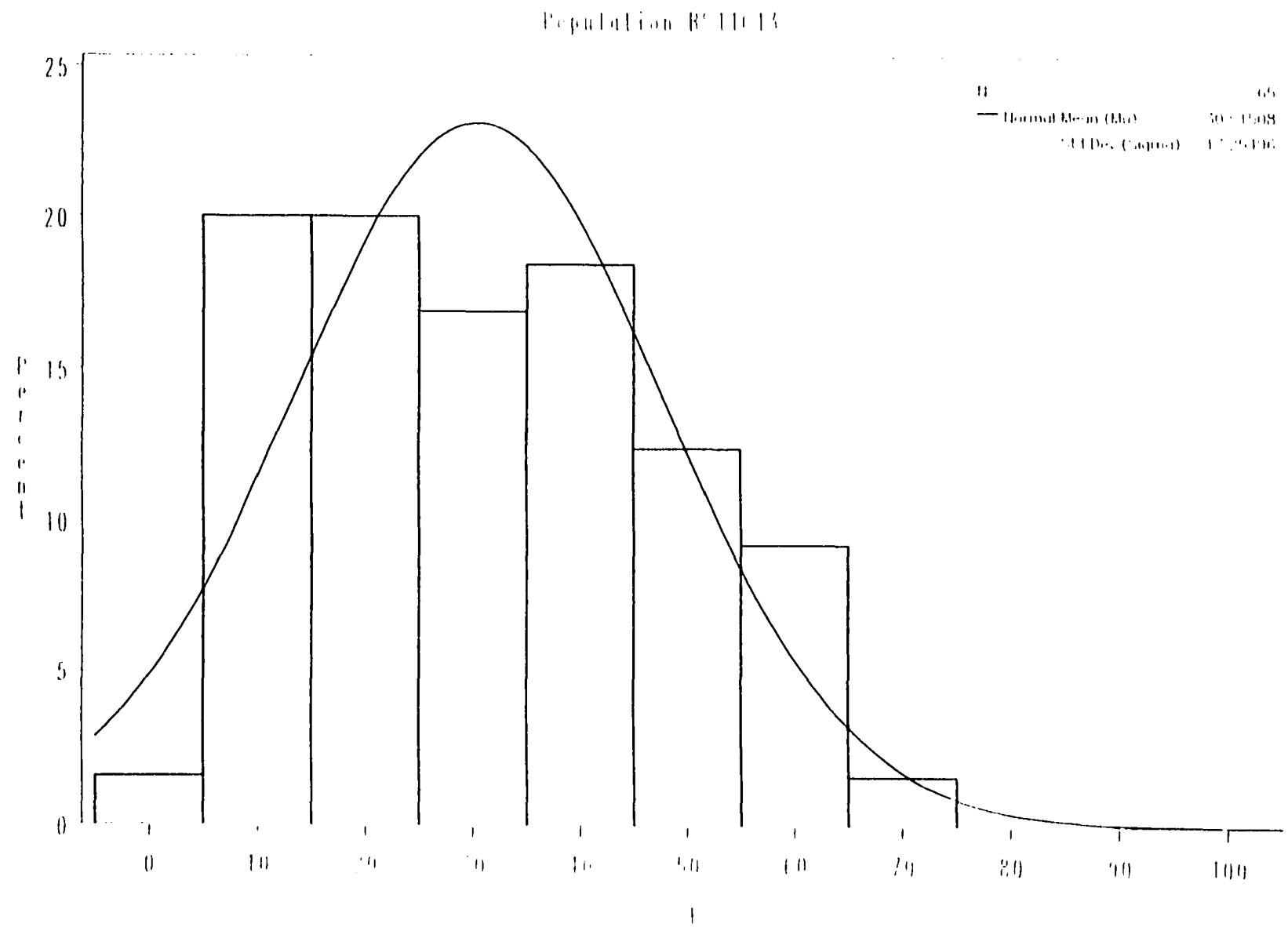


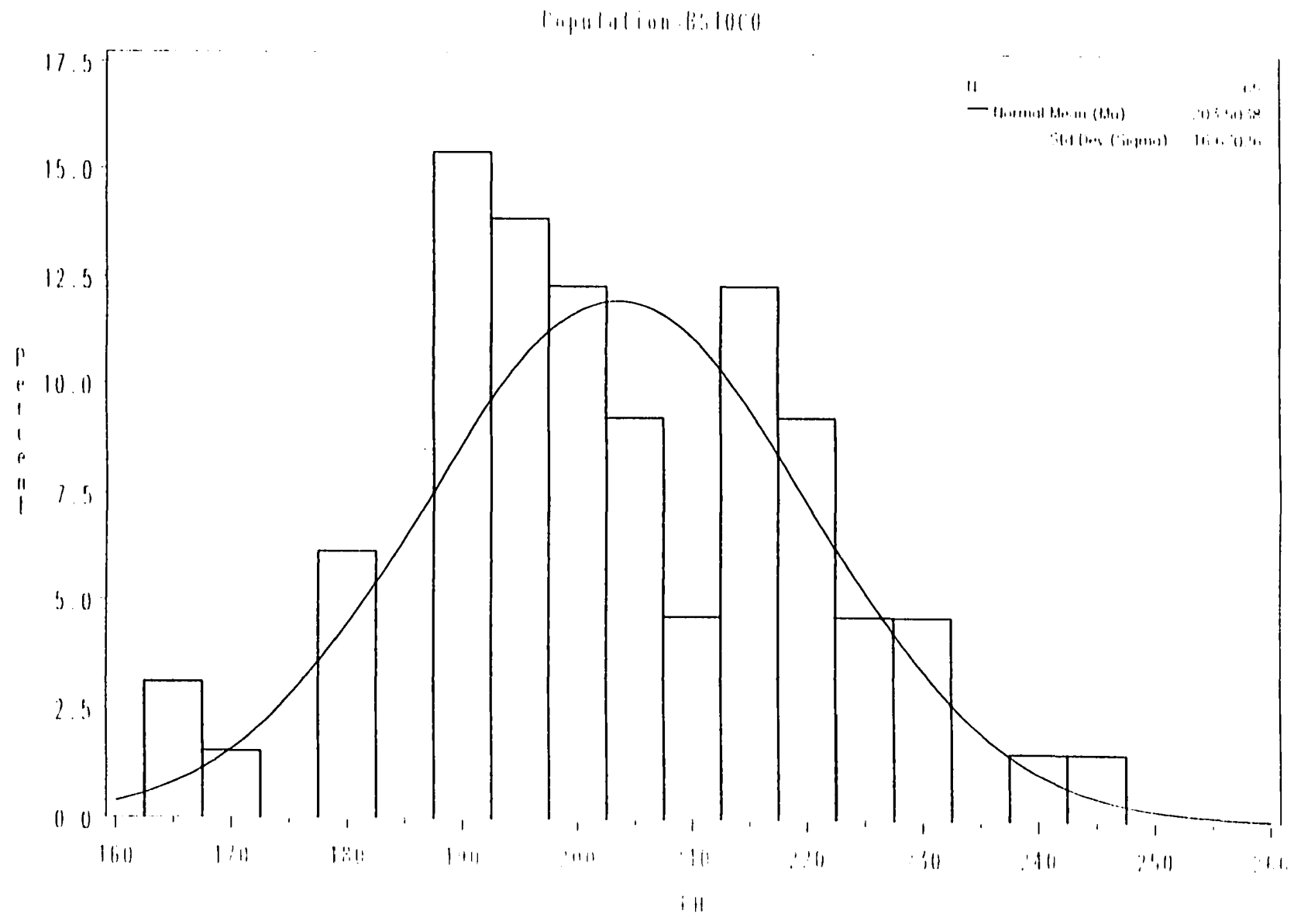


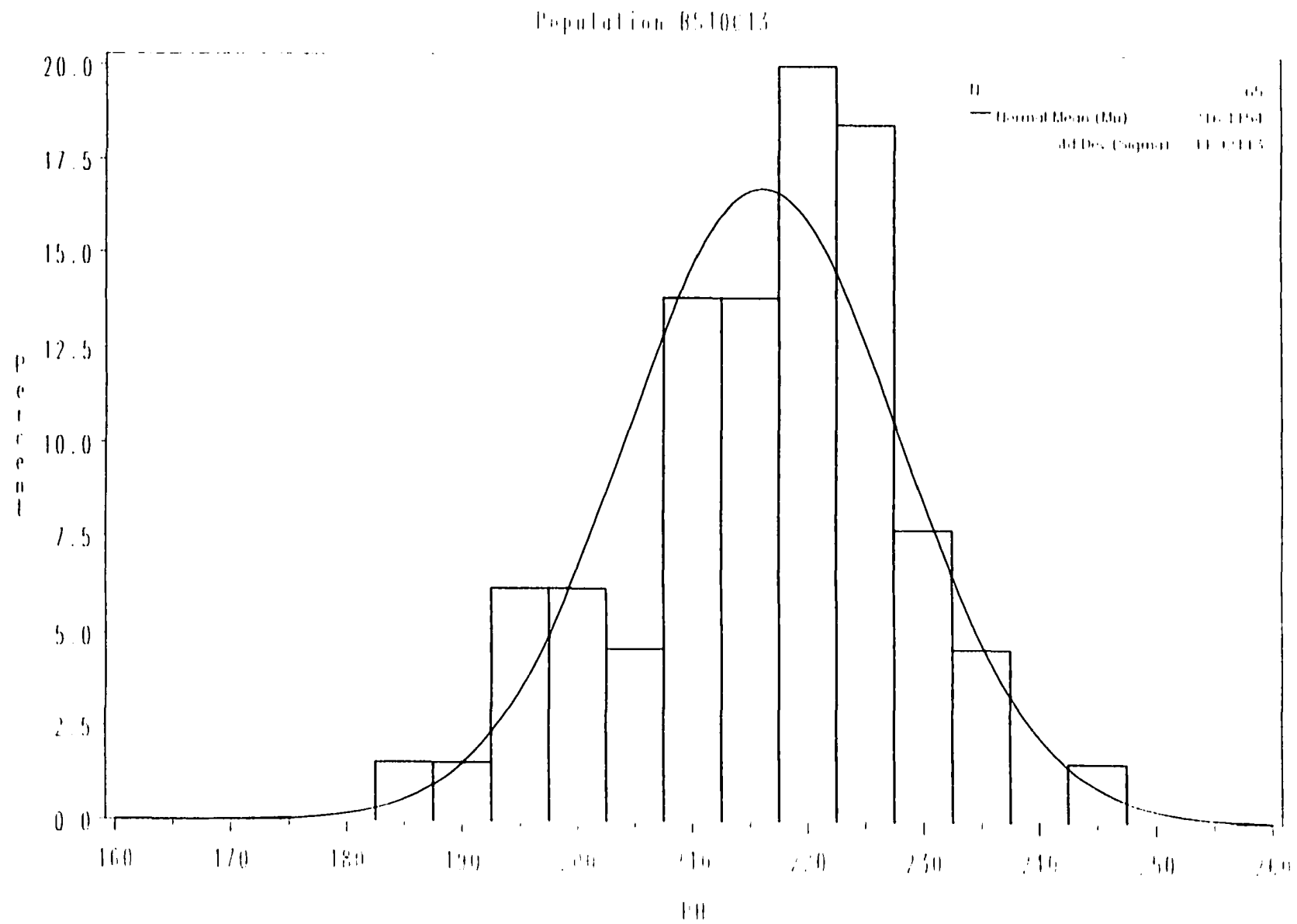
Population B510013



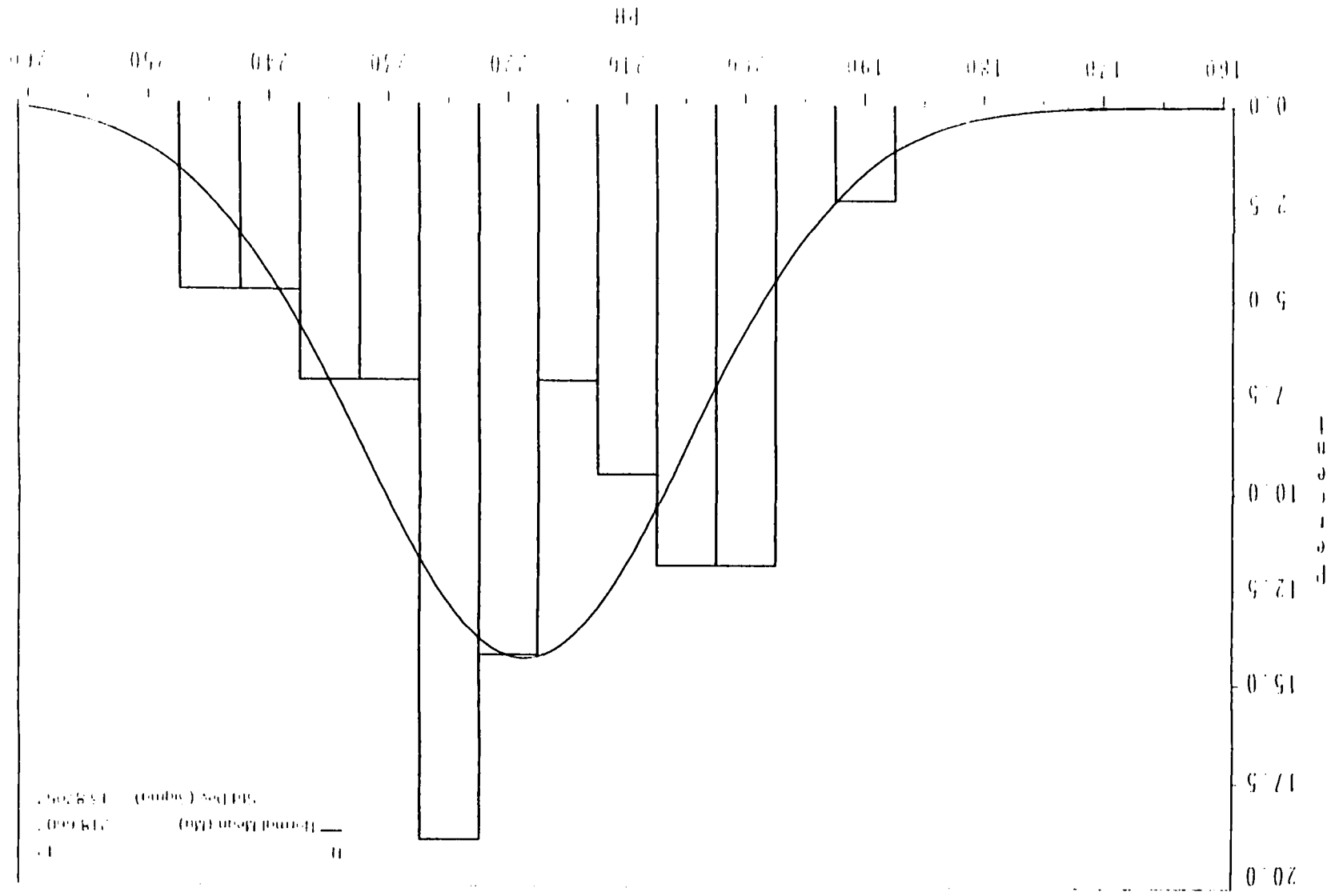




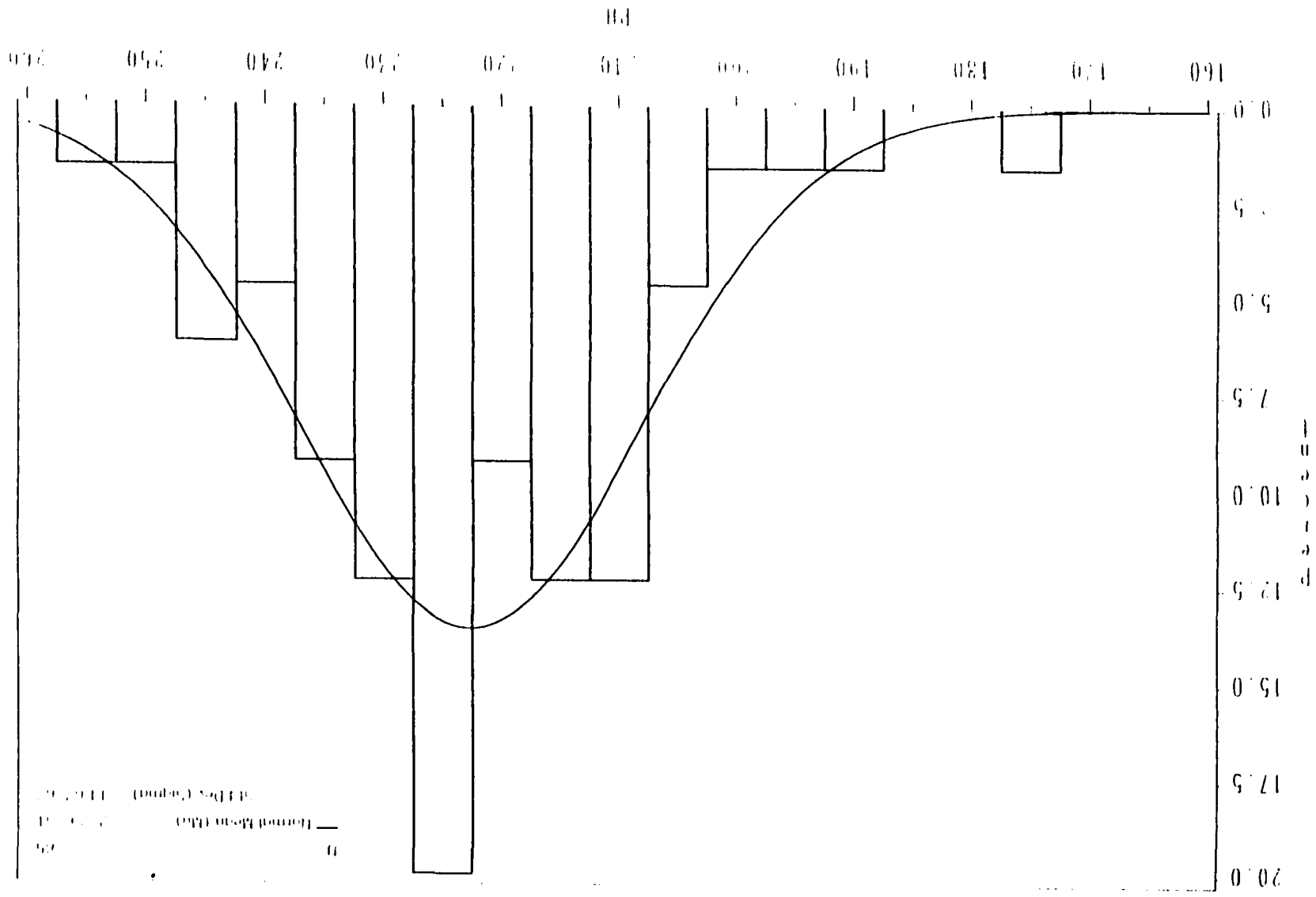


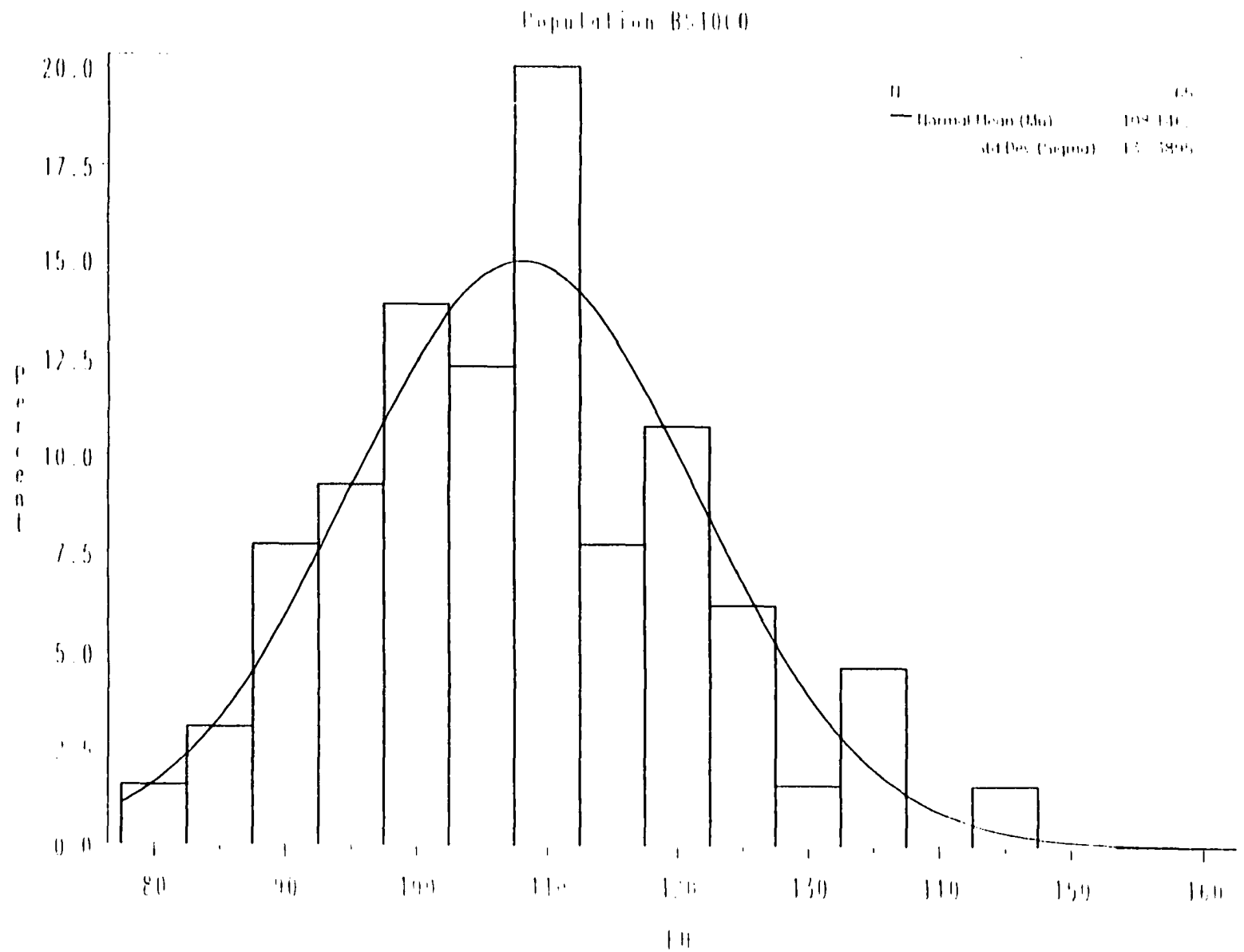


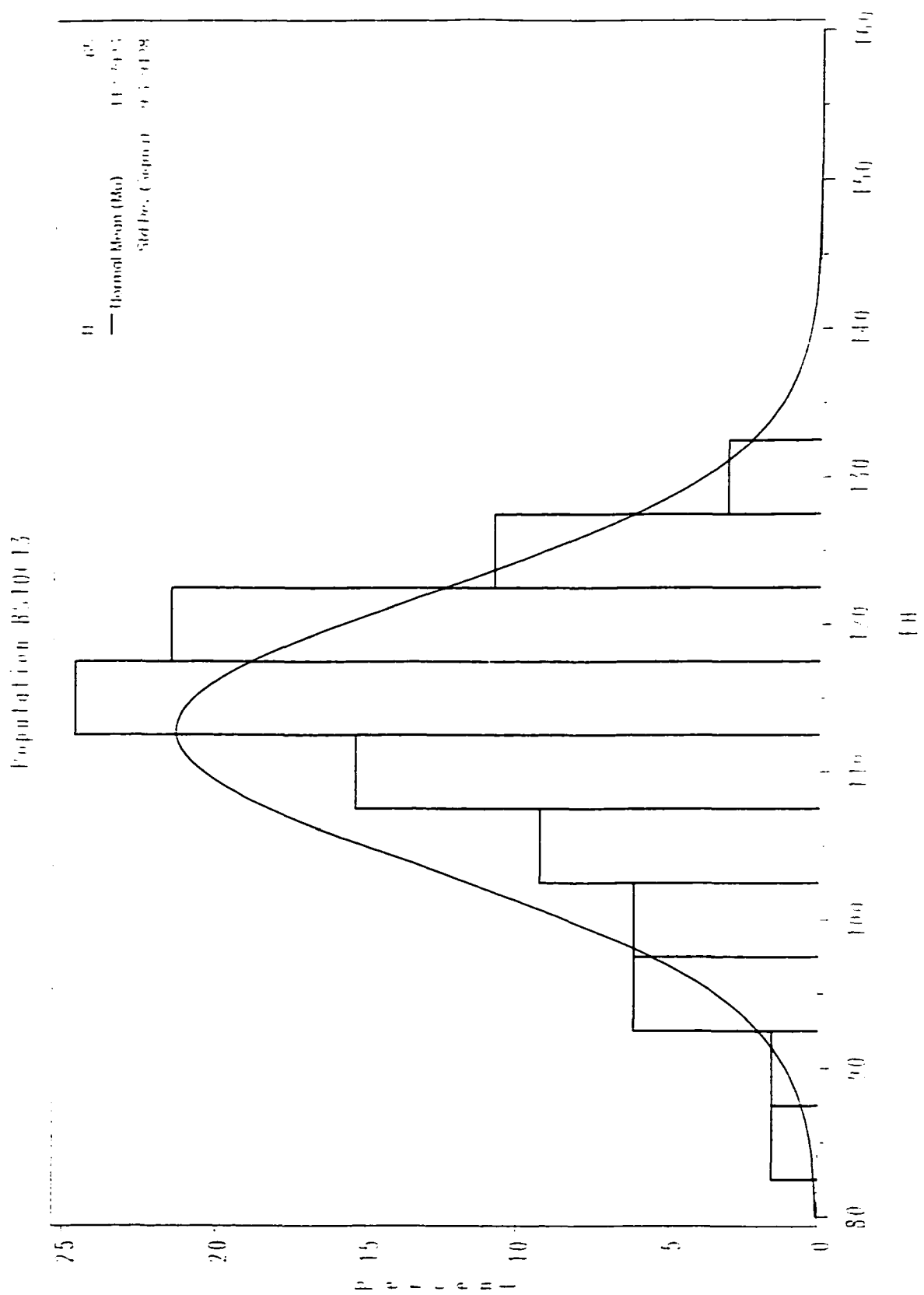
Population B511C0



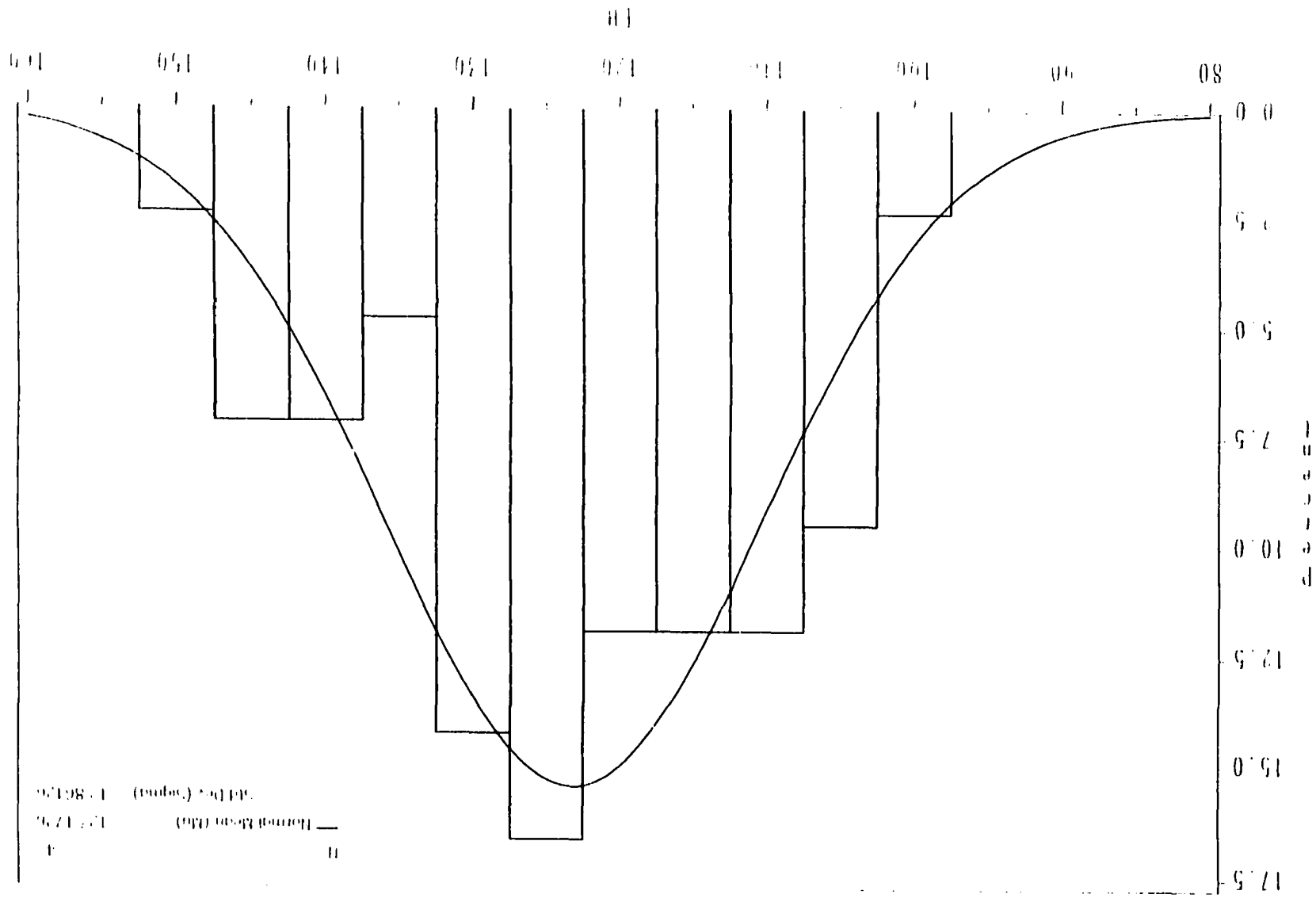
Population (Billion)



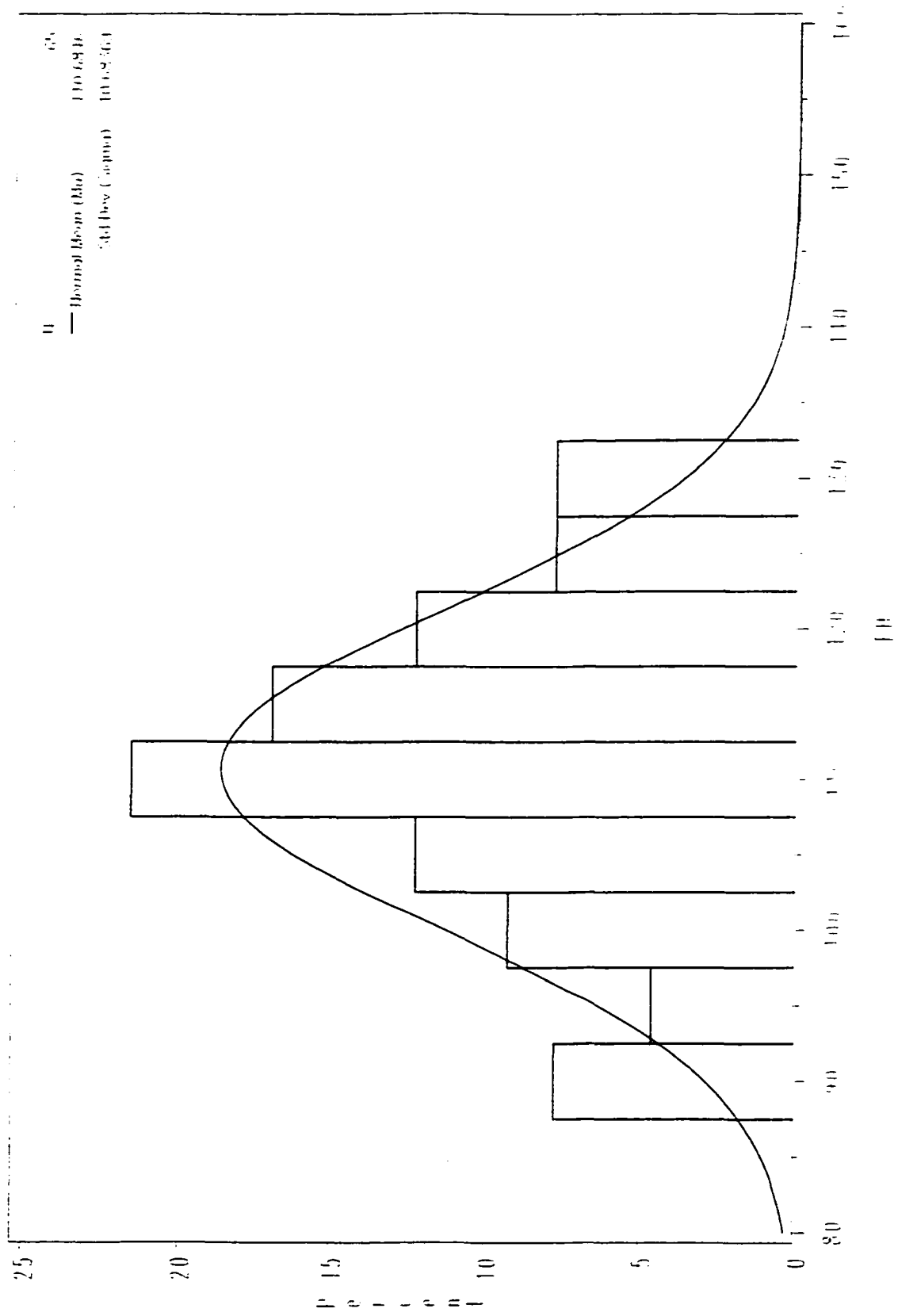


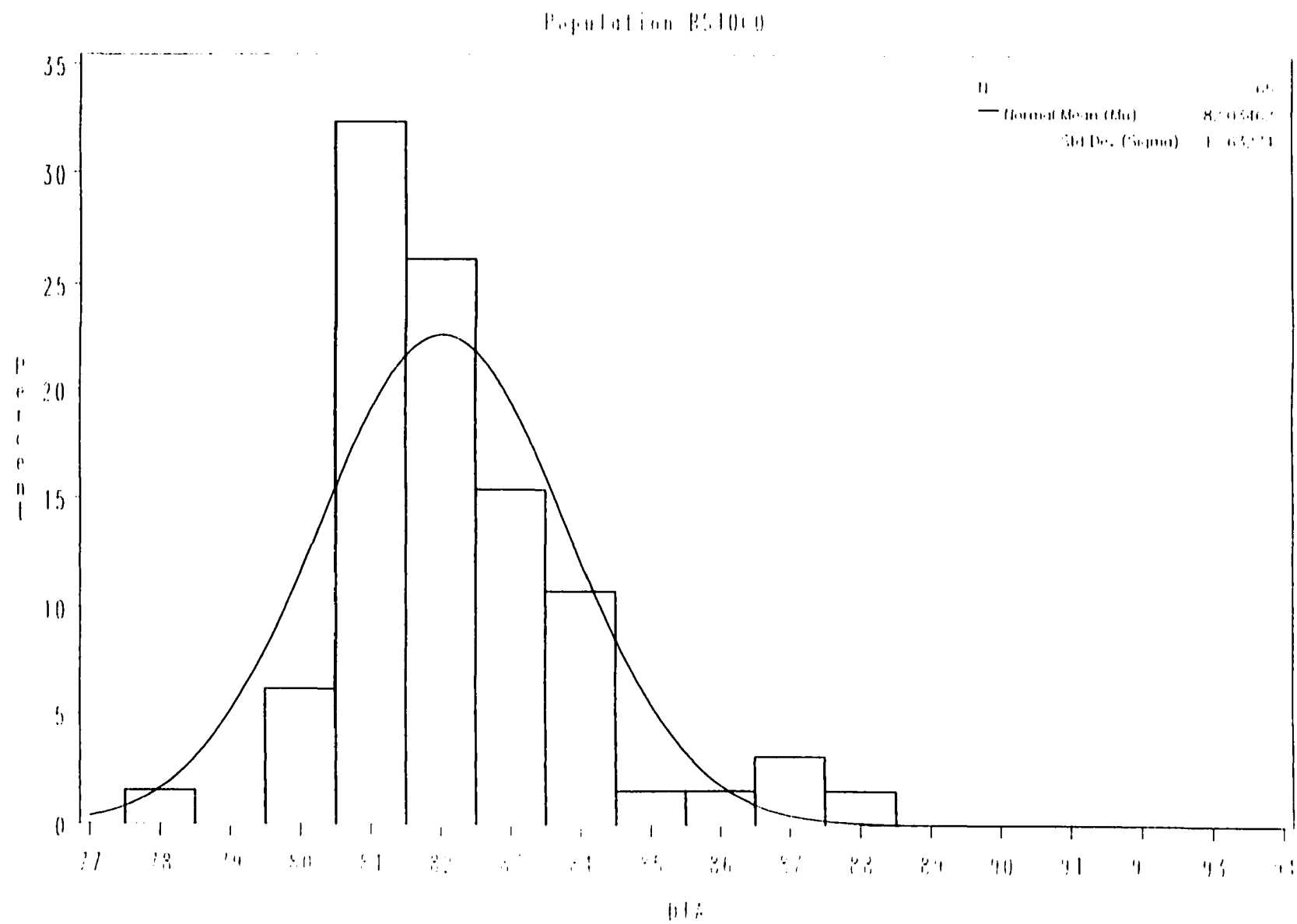


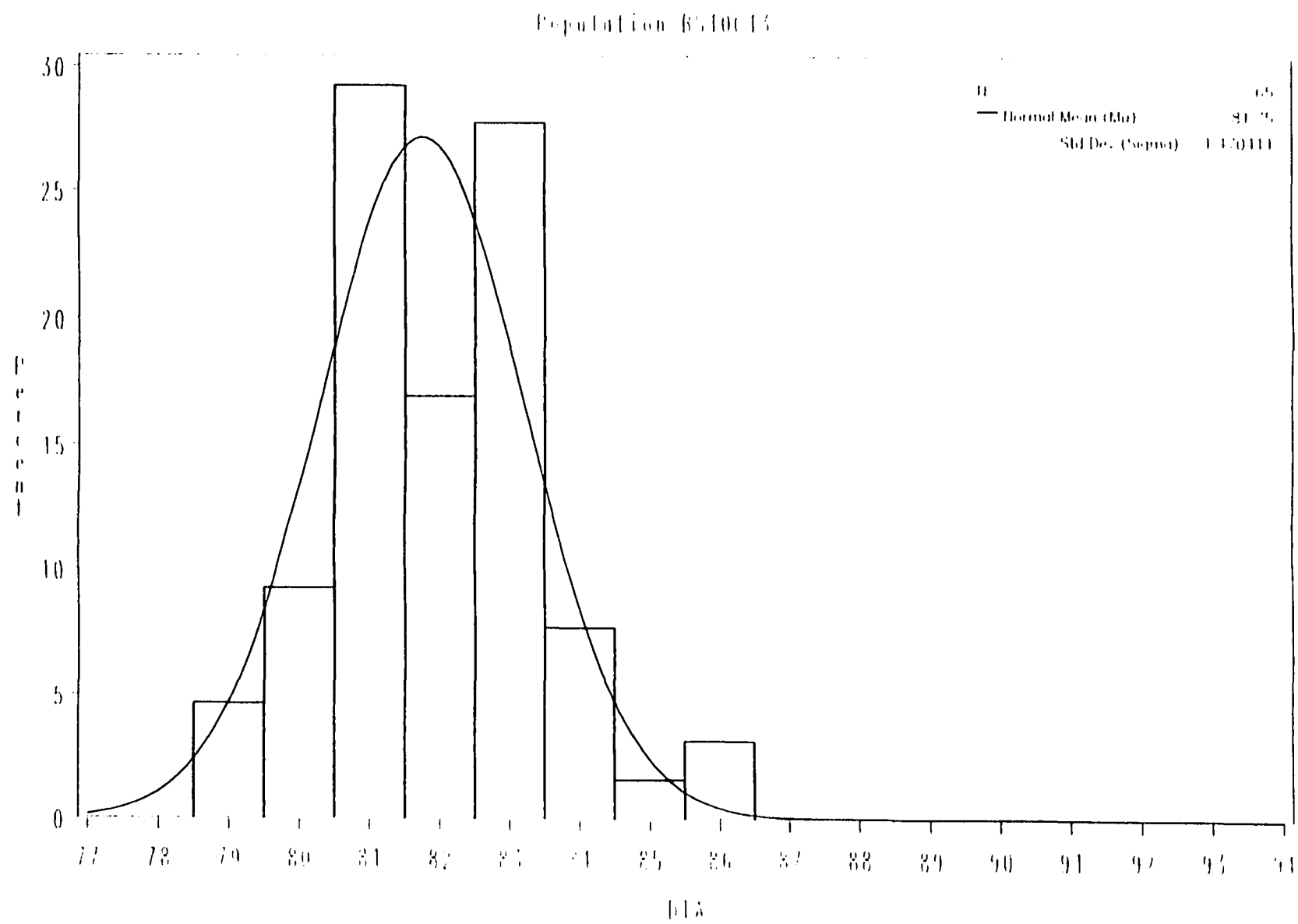
Population Ratio

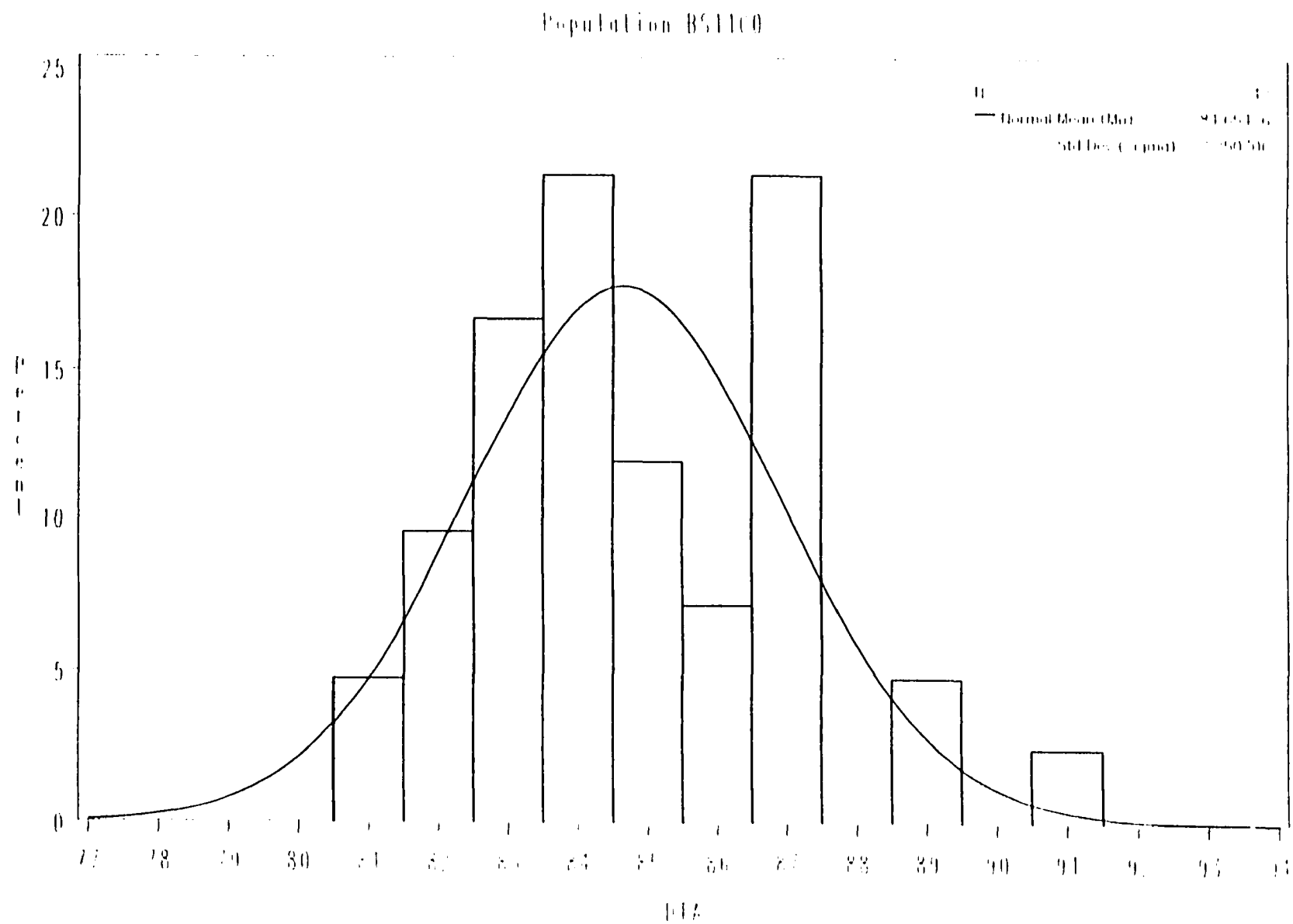


Population BE11C13

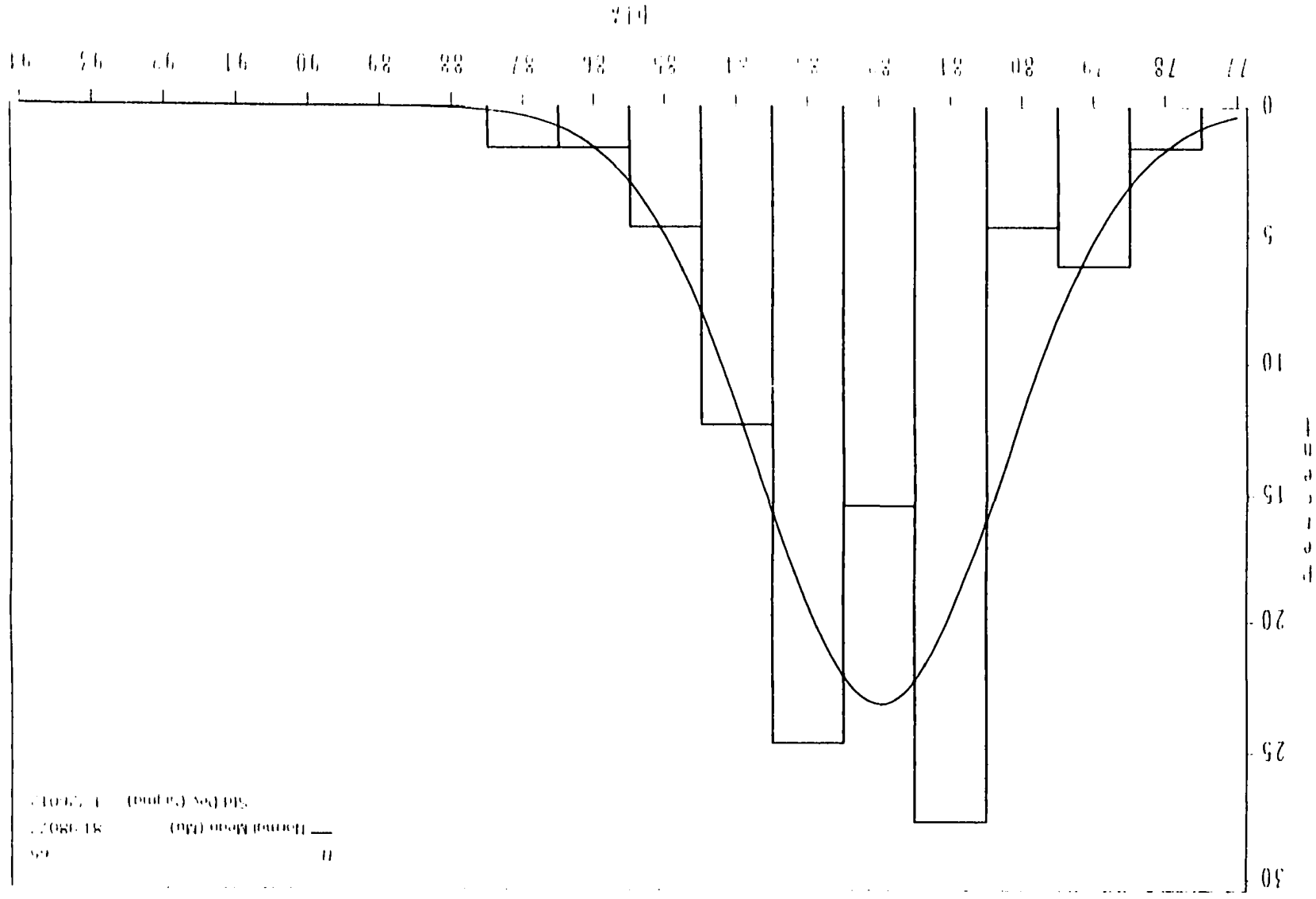


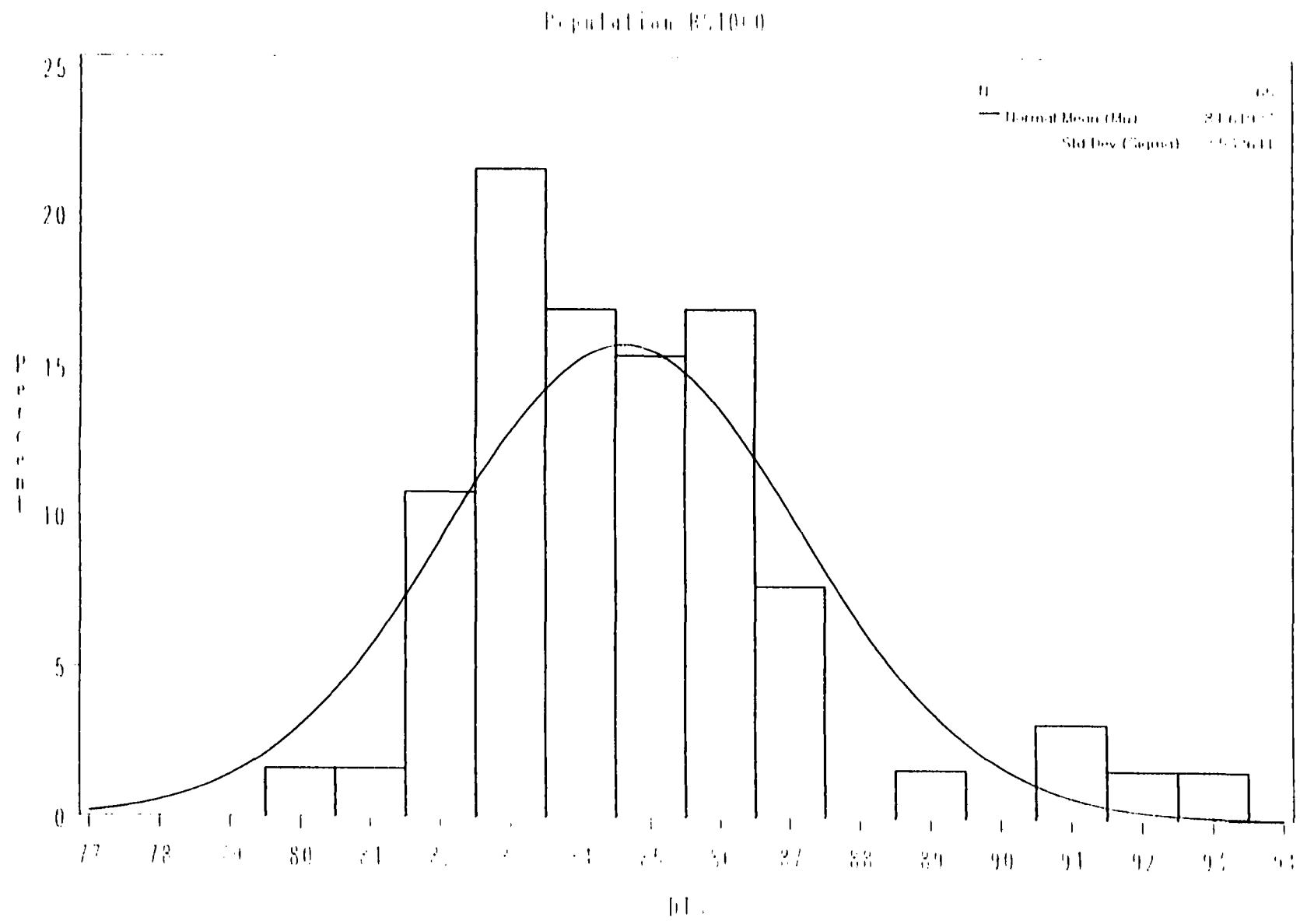


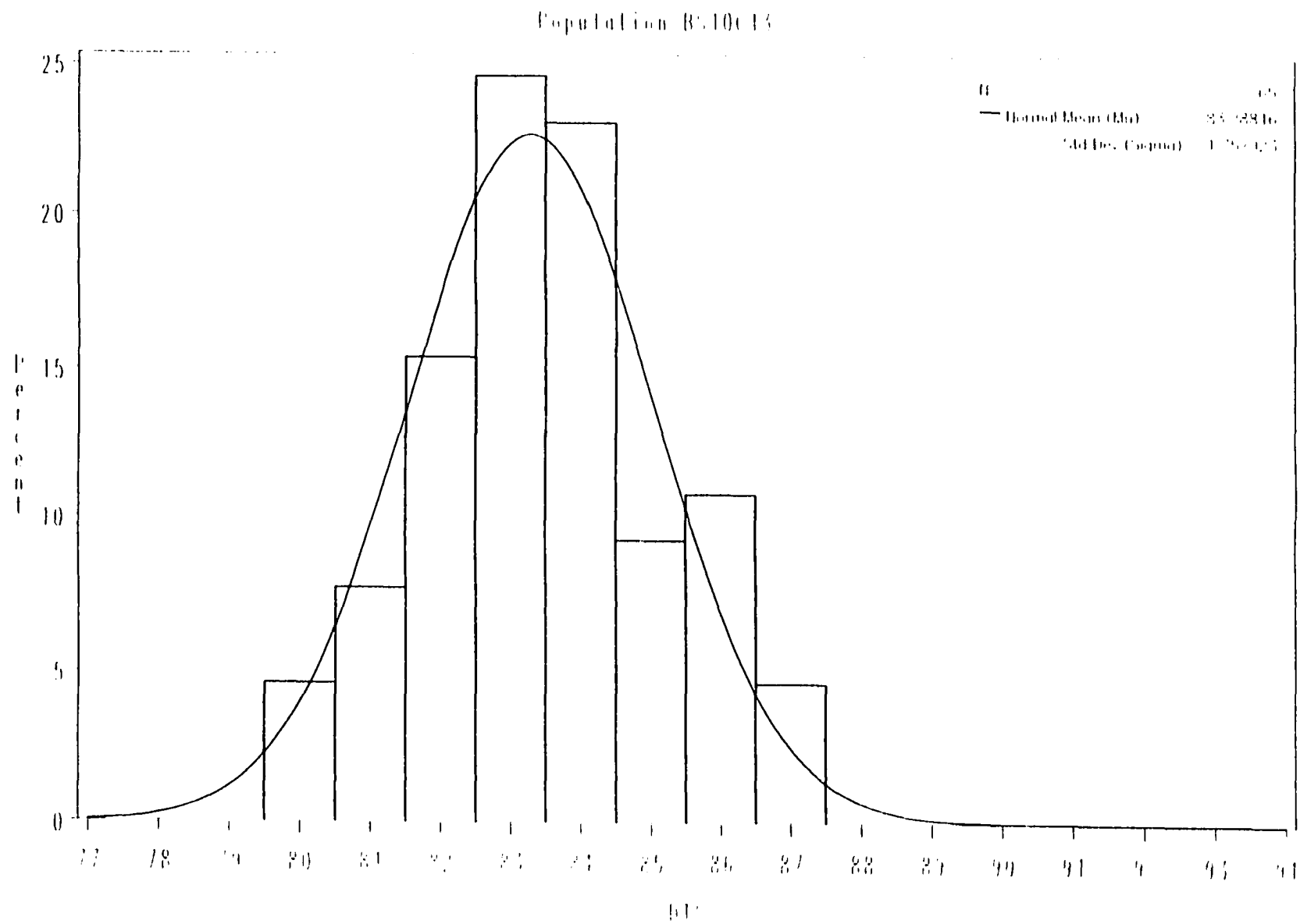


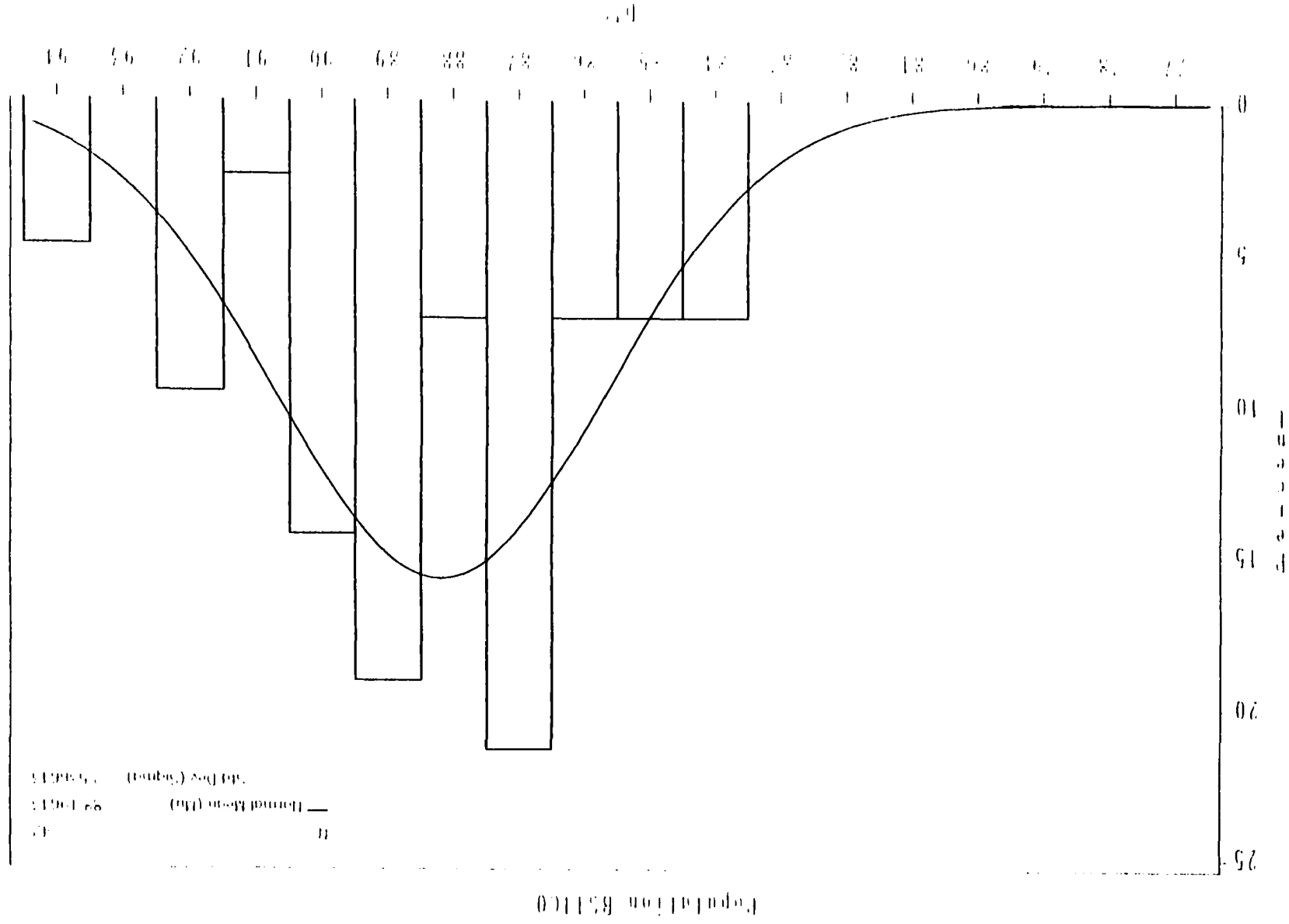


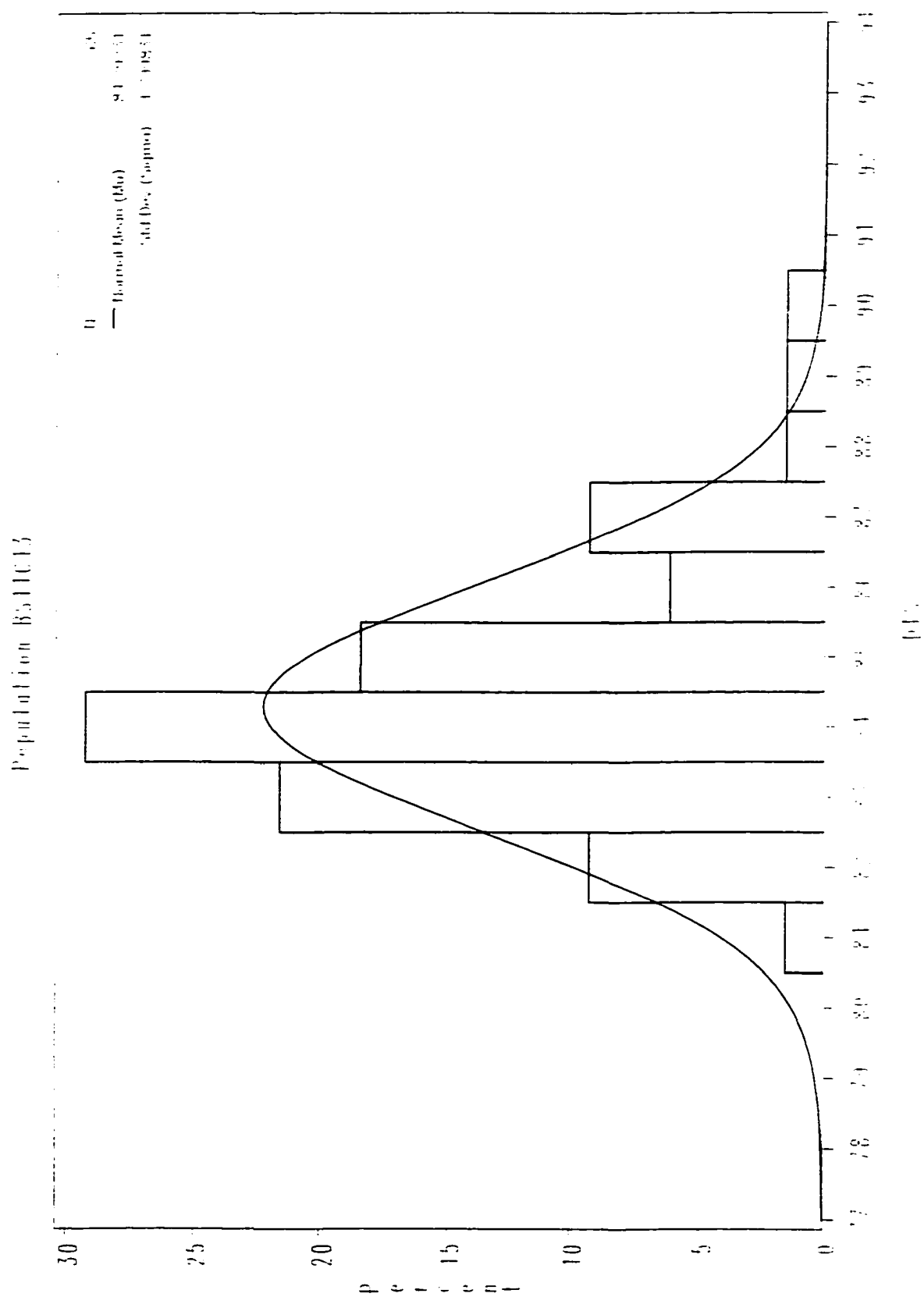
Population-Bulletin 15











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